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REVIEW OF SENESCENCE AS AN IMPORTANT FACTOR DETERMINING THE RELATIONSHIP AMONG AQUATIC PLANTS, THEIR EPIPHYTES, AND PATHOGENS

by

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This report is a review of literature on senescence and relationships between senescence and microorganisms in aquatic plants. The first part of the report summarizes the main facts regarding senescence as follows:

a. Senescence is an important and not very well-understood stage in the life cycle of a plant. It is controlled by internal and external (environmental) factors. The precise mechanism of senescence induction is not known, but, in general, the initiation of senescence involves an imbalance in the relative levels of growth hormones. The change in hormone status can be caused by internal factors or environmental stimuli.

b. Among the environmental stimuli involved in senescence initiation, the following were reported: light, day length, temperature, mineral nutrients, and pathogens.

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When pathogens attack plants, it is not always known whether hormonal imbalances are the cause or the result of infection.

c. Senescence is accompanied by a change in enzyme activities. Peroxidases, glutamate dehydrogenase, endopeptidases, and some hydrolases have been reported to increase their activities during senescence. Dehydrogenase, ribulosebiphosphate carboxylase, glutamine synthetase, and glutamate synthetase generally decrease their activities during senescence.

d. An extensive literature identifies cytokinins as the most generally effective senescence-retarding growth regulators. Abscisic acid (ABA) and ethylene, on the other hand, are known to be promoters of senescence. In many cases, cytokinins and ABA interact in a competitive manner.

e. Decreases in chlorophyll content and protein amount are most often measured as senescence characteristics. Senescence may start long before changes in these parameters become apparent. No universal marker of senescence has been found to date.

The second part of the report describes epiphytic microorganisms on aquatic plants:

a. Aquatic macrophytes often serve as a substratum for epiphytic microorganisms, namely algae, bacteria, and fungi. The amount and diversity of epiphytic microorganisms generally increase with the age of their host, mainly due to the increasing amount of organic matter excreted by the aging host plant.

b. Microorganisms live mostly as commensals (saprophytes) on their hosts but may become parasitic as the hosts undergo stress or approach senescence.

c. In submersed aquatic plants that usually have a very thin and reduced cuticle, bacteria do not need wounds for entry into plants. Bacteria often invade and degrade epidermal cell walls. Some are known to produce lytic enzymes. Some bacteria were reported as being able to produce antibiotics.

d. Fungi are usually regarded as the main decomposers of dead organic matter in aquatic ecosystems. Many fungal species are known to produce enzymes capable of degrading cellulose, pectin, starch, etc. Besides enzymes, some fungi also produce toxins and antibiotics. The phytotoxicity of fungi has a potential use as bioherbicides. In this study, 150 fungal species were reported as being potential parasites on aquatic plants.

e. Epiphytic algae seldom harm their host plants unless the colonization is so dense that it shades plants or, especially in combination with inorganic silt particles, it becomes so heavy that the host plants are damaged and dragged to the bottom.

f. Few viruses were reported from aquatic plants. Viruses may offer an alternative for biological control, but at this point data are insufficient to even consider this possibility.

g. Nematodes contribute to macrophyte degradation in certain cases by wounding the tissue and thus causing easy entry of infection. So far, at least 32 genera of nematodes that were parasitic on aquatic plants have been reported.

Two main points can be made from the literature search: (a) senescence is a process that can be induced by changing the environmental conditions, and (b) plants in the senescent stage are more susceptible to pathogens than young or mature but nonsenescent plants.

The report concludes with recommendations for future research.

PREFACE

This study was conducted as a part of the US Army Corps of Engineers Aquatic Plant Control Research Program (APCRP). Funds for this study were provided by the US Army Corps of Engineers (USACE), under Department of the Army Appropriation No. 96X3122 Construction General. The principal USACE Technical Monitor for the APCRP was Mr. E. Carl Brown.

The principal investigator for this work was Dr. Eliska Rejmankova, Botany Department, University of California, Davis, CA (UC Davis), who prepared this report. The study was conducted under the direct supervision of Dr. Lars Anderson, leader of the Aquatic Weed Research Group, US Department of Agriculture, UC Davis.

This research was monitored at the US Army Engineer Waterways Experiment Station (WES) by Dr. Alfred F. Cofrancesco, Jr., of the Environmental Laboratory (EL), Environmental Resources Division (ERD), Aquatic Habitat Group (AHG). The study was conducted under the general supervision of Dr. John Harrison, Chief, EL, and Dr. Conrad J. Kirby, Chief, ERD, and under the direct supervision of Mr. Edwin A. Theriot, Chief, AHG. Mr. J. Lewis Decell was Manager of the APCRP. This report was edited by Mr. Bobby Odom, while assigned to the Information Technology Laboratory under the Intergovernmental Personnel Act.

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REVIEW OF SENESCENCE AS AN IMPORTANT FACTOR DETERMINING THE RELATIONSHIP AMONG AQUATIC PLANTS, THEIR EPIPHYTES, AND PATHOGENS

PART I: INTRODUCTION

Aquatic Plants and Their Control

1. Even though some problems with aquatic plants existed in previous centuries, the main invasions and spread of nuisance aquatic plants in lakes and in navigation and irrigation canals worldwide have occurred in this century. The two primary reasons for this are (a) increasing water eutrophication and (b) the introduction of alien species into new areas. The time sequence of the most important aquatic plant invasions, together with the methods used for their control, was recently discussed by Anderson (1986).

2. For centuries people tried to control aquatic plants manually, perhaps with the exception of using herbivorous fish in China. With the development and registration of herbicides in the 1950's and 1960's, chemical control has replaced some manual methods. But the application of herbicides has not always been the solution. On the contrary, weed problems have sometimes even increased (Van Zon 1977). Some herbicides used for control of aquatic plants are selective, which means that other weeds usually replace those controlled. In stagnant waters, the decomposition of herbicide-killed plants leads to a further increase in eutrophication. The use of chemical compounds in water is requiring stricter regulations because of possible side effects and potential ground-water contamination. Unsatisfactory results with chemical aquatic plant control and increasing costs of herbicides have stimulated the search for new, alternative methods.

3. Many attempts have been made to regulate and restrict nuisance weed growth using either a selective biological agent (pathogenic bacteria and fungi, viruses, nematodes, insects, allelopathic plants) or herbivorous organisms. Several large-scale research programs on biological control of aquatic plants were started in the early seventies (Freeman et al. 1974, 1981; Bennett 1977). Many of them have been successful; for example, the fungus *Cercospora rodmanii* was used for control of waterhyacinth (Pennington and Theriot 1982),

and the alligatorweed flea beetle and alligatorweed stem borer were used as control agents for alligatorweed, *Alternanthera philoxeroides* (Cofrancesco 1984). Most recently, excellent control of *Salvinia molesta* in Australia was obtained with the introduction of the weevil *Cyrtobagous salviniae* (Room 1986). Many other projects that looked very promising in laboratory tests failed large-scale trials in the field. A new possible approach to biocontrol of aquatic plants seems to be the application of genetic engineering technology (Pennington 1985).

4. In the last few years, integrated management of aquatic weeds combining several control methods has been stressed. For example, the combination of insects (waterhyacinth weevils and waterhyacinth moths) with the parasitic fungus (*C. rodmanii*) was used for controlling waterhyacinth in Louisiana (Sanders and Theriot 1985). These control agents have to be combined in such a way that they act synergistically. Insects often damage the leaves of aquatic plants and provide points of entry for pathogenic fungi or bacteria (Charudattan et al. 1978). Recently, Charudattan (1986) described integrated control of waterhyacinth using a pathogen, insects, and sublethal rates of herbicide. The US Environmental Protection Agency (EPA) sponsored several projects summarizing integrated pest control research and methodology (Tyndall et al. 1981; Aurand 1982, 1983; Trudeau 1982; Tyndall 1982).

History of Natural Macrophyte Decline

5. Dramatic changes have been observed in aquatic plant populations in the last several decades. New, introduced species have become established while others have disappeared. Increasingly disturbed aquatic ecosystems are more susceptible to sudden invasions. Introduced species often thrive at first, being free of natural parasites and foraging animals from their native locations. After a few years, however, a sudden outburst of growth is often followed by an almost equally sudden decline of most of the population; e.g., a rapid spread of *S. molesta* in Lake Kariba was followed by its degeneration (Loveless 1969), expansion of *Myriophyllum spicatum* in Chesapeake Bay in the late fifties to early sixties was followed by its decline in the mid seventies (Bayley et al. 1978; Orth and Moore 1984), and similar situations occurred in lakes in Wisconsin a few years later (Carpenter 1980b, Jones et al. 1983). A sudden decline of *Hydrilla verticillata* was described from Orange Lake, FL

(Haller 1983). Reasons for this reduction were not entirely known, but higher water level most probably played a major role.

6. Declines have been observed not only in populations of introduced aquatic macrophytes but in native species as well. In the 1930's an epidemic of the so-called "wasting disease" almost entirely destroyed the normally dense beds of marine eelgrass, *Zostera marina*, along the Atlantic coast of North America and Europe (Renn 1936, Rasmussen 1977). Motta (1978) described a considerable decline of *Potamogeton perfoliatus* and *Ruppia maritima* in Chesapeake Bay. *Myriophyllum spicatum* and *P. perfoliatus* stands are decreasing drastically in Neusiedlersee in Austria (Schiemer and Prosser 1976); Jupp and Spence (1977) described the decline in submersed macrophyte growth in Loch Leven. Increased occurrence of sudden macrophyte death was described in lakes in Norway (Rorslett 1985) as well as in a fjord in Denmark (Kiorboe 1980b). Marked regression has occurred in the growth of *Potamogeton pectinatus* in Swartvlei Lake in South Africa (Taylor 1983).

7. None of these declines has a simple cause, and none has been adequately explained. Declines always occur because of a combination of several interacting factors. Dozens of papers were published offering various explanations of drastic *Zostera* decline; the first and still most widely held view is that the mass destruction was the result of a disease caused by one or more parasitic organisms (the fungus *Ophiobolus halimus* or slime mold *Labyrinthula macrocystis*). It has never been proved that any of the organisms found in dead eelgrass can directly cause disease and subsequent death of the plant. After reviewing the literature on *Zostera* and the "wasting disease," Rasmussen (1977) suggested that temperature may play a decisive role in the destruction of the eelgrass. He also pointed out that once the plants are weakened by unfavorable temperatures (or any other environmental factor), then the so-far saprophytic microorganisms may become pathogenic and speed up the senescence and decay.

8. Decline in *M. spicatum* in Chesapeake Bay was believed to have been caused by viruses or virus-like particles (Bayley et al. 1968); two sets of symptoms were designated as "Northeast Disease" and "Lake Venice Disease." In later studies, Bayley (1970) was not able to identify the causal agent for any of them. Bean et al. (1973) were unable to produce symptoms of "Lake Venice Disease" either by direct inoculation of healthy plants with extracts from diseased plants or by growing diseased and healthy plants in the same

container. Only plants grown under low light intensity and inoculated with extracts from diseased tissue produced symptoms resembling those of "Lake Venice Disease." Plants growing under stress conditions (low light intensity) were apparently more susceptible to attack by microorganisms.

9. Carpenter (1980b) explained that no single factor can be responsible for the decline of *M. spicatum* in Lake Wingra, WI. He suggested that the most probable causes were increased turbidity, shading by epiphytes, and, possibly, increased susceptibility to parasites. Jones et al. (1983) presented a growth model of *M. spicatum* in Lake Wingra that predicted a substantial decline in macrophyte biomass due to phytoplankton increase. Available data do not show whether the phytoplankton increase preceded or followed the macrophyte decline.

10. Phillips et al. (1978) discussed the hypothesis that increasing phytoplankton biomass following eutrophication absorbs enough light to prevent net photosynthesis by aquatic macrophytes. These authors suggested, however, that the situation is more complicated. First, increasing epiphyte growth and increasing growth of a blanketing mass of filamentous algae will reduce the light intensity available to macrophytes so that a greater proportion of fixed energy is required for maintenance, and less is available for growth. Phillips et al. (1978) also considered the suppressive influence of organic secretions by the macrophytes on phytoplankton as shown, e.g., by Fitzgerald (1969). As their growth decreases, the influence of macrophytes on the phytoplankton diminishes, and increasing growth of phytoplankton will further reduce the light available to the macrophytes.

11. A resource allocation hypothesis for macrophytes decline was offered by Johnstone (1982). He suggested that a switch in resource allocation from vegetative growth to sexual reproduction, along with a limited ability of the mature stand to replace itself, ultimately causes the species to decline in abundance. If this hypothesis is correct, control methods that stimulate the vegetative growth of these plants (harvesting) may effectively prolong the aquatic weed problem.

12. Macrophyte development in a eutrophic lake in western New York (Nicholson 1981), influenced by repeated herbicide applications and mechanical cutting, showed that, indeed, species capable of vigorous regeneration (*M. spicatum, Ceratophyllum demersum, Elodea canadensis*) were not substantially affected by herbicides and in several years dominated over native *Potamogeton*.

Nicholson pointed out that species with characteristics like: (a) poor regeneration from detached pieces, (b) emphasized sexual reproduction, and (c) poor regrowth and heeling when cut would be most vulnerable to mechanical cutting. When he compared the healing capacities of *M. spicatum* and native *Potamogeton*, he found that *M. spicatum* heals and elongates rapidly while *Potamogeton* often suffer local tissue deterioration. *Myriophyllum spicatum* is known to produce phenolic compounds (Planas et al. 1981) that are deterrent to herbivores and pathogens, which may be the reason for its local advantage over *Potamogeton*.

Management of Aquatic Weeds Based on Their Life Strategies

13. Throughout their life cycles, plants exhibit sensitivity to environmental factors and are capable of a range of responses to the environmental fluctuations. Different stages of plant development and different physiological processes may have different temperature and light optima and may require different photoperiods. Also, the sensitivity to infection by pathogenic fungi or bacteria is not the same throughout the plant's life cycle. Therefore, an understanding of the biology and physiology of problematic aquatic species is a necessary basis for their successful management.

14. Much information on the physiological ecology of aquatic plants already exists (Spence 1972; Barko and Smart 1981; Titus and Stone 1982; Barko et al. 1984, 1986; Agami and Waise 1985). Some of the papers refer to new management possibilities using photoinhibition of reproductive organ formation (Klaine and Ward 1984; Spencer and Anderson 1986a, b) or naturally occurring competitive plants (Yeo and Thurston 1984). Anderson (1986) outlines future approaches and principles in aquatic plant management based mainly on manipulation of external factors with the aim to disrupt the life cycle of a plant.

15. Senescence is an important and not very well-understood stage in the life cycle of a plant. With a few exceptions, not much is known about the factors that influence or trigger senescence in aquatic macrophytes. Reports indicate that senescent plants are probably most susceptible to infections by pathogens (Leopold 1961; Bean et al. 1973; Rejmankova 1979; Sharma 1985).

16. This report has been prepared with the aim of reviewing the available information on senescence of aquatic macrophytes and on microorganisms involved in the senescence process.

PART II: SENESCENCE

Background

17. Death of an organ or of the whole plant is always preceded by the process of senescence, which may be regarded as the final phase in development that leads to cellular breakdown and death (Wareing and Phillips 1985). More precisely, in leaves, it relates to the loss of structural integrity and photosynthetic competence of the chloroplasts. Senescence is also defined as the phenotypic manifestation of deleterious effects accumulating in old age, namely errors committed by the molecular genetic apparatus during protein synthesis (Leshem 1986). The term "senescence" has a somewhat confusing overlap in meaning with the term "aging." According to Leopold (1975), senescence refers to the deteriorative processes that are natural causes of death whereas aging refers to the wider array of processes of accruing maturity with the passage of time, without referring to death as a consequence. Of the steps in biological development, senescence is one of the least defined (Leopold 1961). Changes in growth rates and vigor and increases in susceptibility to environmental stress or pathogens are generally connected with senescence.

18. Before considering plant senescence further, it is necessary to distinguish between monocarpic species, which flower and fruit only once and then die, and polycarpic plants, which flower and fruit repeatedly. Monocarpic species include all annual and biennial plants and a certain number of perennial plants that grow vegetatively for a number of years and then suddenly flower, fruit, and die. Thus, in monocarpic species, death of the whole plant is closely connected with reproduction and is evidently genetically determined to occur at this stage of the life cycle. On the contrary, in polycarpic species, death of the whole plant is not normally associated with reproduction, and there is a great variation among the different individuals of a given species with respect to the length of the life span.

19. Another convenient distinction is between organ senescence and whole plant senescence. In most plants, each leaf has only a limited life span so that as the shoot continues to grow in height, the older leaves at the base tend to senesce and die. This pattern of senescence has been described as sequential senescence, and it must be distinguished from simultaneous or synchronous senescence (e.g., leaves of temperate deciduous trees).

20. Figure 1 illustrates the parts of a plant that can undergo senescence during its life. The submersed aquatic plant *M. spicatum* is shown in the picture.

21. Various internal factors of the plant are involved in the regulation of senescence (hormones, growth regulators), and a number of external factors may affect the rate of senescence, including light intensity and day length, mineral nutrition, disease, etc.

22. The precise mechanism of senescence induction is not known (Biswal and Biswal 1984). Factors influencing the initiation of senescence and the initiating events are described in detail by Thomas and Stoddart (1980), who

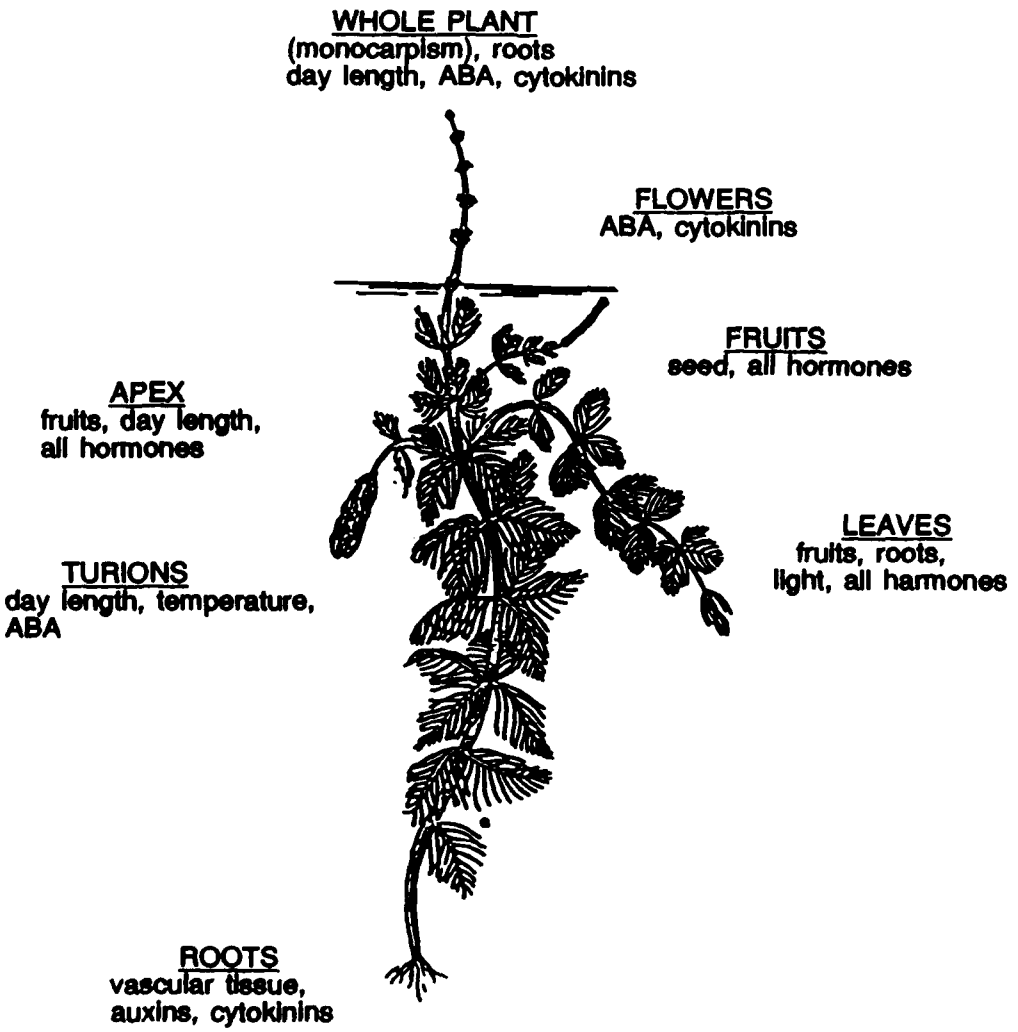

Figure 1. Parts of a submersed aquatic plant that can undergo senescence. Environmental and hormonal influences are indicated together with those parts of the plant that can exhibit correlative controls

emphasized the regulatory aspects of senescence and its characterization as a genetically directed process. These authors described the following factors:

a. Genetic. Senescence is an integral part of plant development and, therefore, subject to direct genetic control. To what extent the control is directed from the genome of either the nucleus, chloroplast, or mitochondria has been a subject of many studies and discussions and is not clear yet (Osborne and Cheah 1982).

b. Correlative. Senescence may be induced in a given organ (leaf) as a direct consequence of its position relative to other organs. It is a result of competition among different organs of a plant for light, space, translocated nutrients, and growth regulators.

c. Environmental. Many experiments have been done in an attempt to assess the role of environmental factors in initiating or delaying senescence. Exposure to low light promotes senescence. Senescence is also influenced by day length. Exposure to adverse temperature in either the high or low range can bring about a senescencelike response, presumably as a consequence of structural or metabolic damage. Deficiency in mineral nutrition results often in chlorosis, necrosis, and leaf senescence. Often senescence appears to be induced in a direct response to a deficiency resulting in redistribution of the limiting nutrients from older tissues to developing structures. This is particularly a case of the mobile elements nitrogen, phosphorus, potassium, magnesium, sodium, and chlorine. The presence of pathogens within a leaf can result in acceleration of senescence.

23. Light is without any doubt one of the most important environmental factors, and its role in photosynthesis, plant development, and morphogenesis has been thoroughly studied. However, nothing definite is known about the mechanism of light action in controlling senescence although it has been known either to stimulate or retard this process. Biswal and Biswal (1984) reviewed the present knowledge on photocontrol of leaf senescence. Photostimulation of senescence is usually a question of high light intensities that may lead to photobleaching of chlorophylls. High light intensities not only accelerate chlorophyll breakdown but also lead to ultrastructural modifications and loss in soluble carbohydrates. The action of light in controlling senescence is normally attributed to its effect in delaying senescence. The action of light in retarding senescence has been attributed by many authors to its role in photosynthetic production of organic nutrients. Theories also suggest that phytochromes regulate leaf senescence. Another possibility is that light may induce changes in the level of phytohormones that influence senescence.

24. Senescencelike symptoms caused by nutrient deficiency (namely nitrogen) have been demonstrated in many plants. Jackson and Drew (1984) describe

the accelerated senescence in flooded plants. They stress nitrogen deficiency as a factor responsible for early senescence. Deficiency of nitrogen was suggested as being responsible for an early senescence of detached shoots of *Myriophyllum verticillatum* that were dependent on the nitrogen supply from nutrient-poor water as opposed to the rooted shoots that obtained enough nitrogen from sediments (Weber and Nooden 1974). High concentrations of CO_2 are known to increase the biomass production and accelerate senescence in terrestrial plants (Omar and Horvath 1983).

25. Present knowledge of the physiology and biochemistry of senescence is derived mainly from studies on leaves (both attached and detached leaves or leaf discs). Woolhouse and Jenkins (1983), however, warn against broad generalizations based on results of experiments that were done on relatively few plant species. The physiological responses, metabolic changes, or regulatory mechanisms involved in senescence will not be the same for plants adapted to totally different types of habitats (for aquatic macrophytes, a plant species growing in nutrient-poor oligotrophic lake with a high light penetration as opposed to a plant from nutrient-rich, eutrophic pond with a high turbidity).

26. The role enzymes play in leaf senescence was reviewed by Lauriere (1983). The main groups of enzymes studied were hydrolases, ribulosebiphosphate carboxylase (RuBPC) and the enzymes of the Calvin-Benson cycle, and a limited number of other enzymes, especially oxidoreductases. Increased cellular hydrolase activity has often been presented as one of the various manifestations of senescence, in accordance with the degradative nature of the process. Not all hydrolases, however, undergo an increase during the senescence, and again, there are differences among different plant species.

27. The enzyme with the most well-known control during senescence is RuBPC, which is responsible for net photosynthetic CO_2 fixation. The activity of RuBPC reaches its maximum at the time of completion of leaf expansion; then it declines to only about 5 percent of maximum activity at the time of advanced senescence (Batt and Woolhouse 1975). This level of enzyme activity represents the major loss of soluble protein during senescence (Friedrych and Huffaker 1980). It seems probable that the loss of RuBPC is the primary event responsible for the decrease of photosynthesis (Thomas et al. 1978).

28. Among the other enzymes, dehydrogenases have been studied most. A decrease in their overall activity is generally observed during the last stages of senescence. An increase in overall peroxidase activity during

senescence has often been reported. Current research is oriented toward the determination of the capacity of peroxidases to eliminate hydrogen peroxide, the production of which increases during senescence (Birecka et al. 1979) and which is toxic to plant cells. Nitrate and nitrite reductases have been little studied during senescence. A considerable increase in the activity of glutamate dehydrogenase has been shown by several authors. An increased activity of endopeptidases during senescence has been reported (Keist and Feller 1984).

29. Growth regulators such as cytokinins, auxins, gibberellins, abscisic acid (ABA), and ethylene are all known to play some role in senescence, but there is no firm knowledge on their modes of action. A major action of plant hormones in regulating senescence has been attributed to their activity in regulating the opening or closing of leaf stomata (Osborne and Cheah 1982).

30. Both cytokinins and gibberellins are known to delay senescence in many different plant species. This effect was described for excised leaves as well as for leaves attached to the plant (Smith and Grierson 1982). ABA, on the other hand, has been found to accelerate senescence in leaves of many species (Colquhoun and Hillman 1972). In most cases, cytokinins and ABA interact in a competitive manner.

31. There is contradictory evidence concerning the effect of ethylene on the rate of senescence. It has been shown that ethylene induces senescence in leaves of certain species and that it is also produced by senescing leaves of those species (Gepstein and Thimann 1981); however, ethylene may be without effect in another species. According to Osborne (1984), the amount of ethylene in some senescing aquatic plants increases, but whether or not the increased amount of ethylene causes the senescence in those plants is not known.

32. Manos and Goldthwaite (1975) demonstrated a seasonal senescence cycle in excised mature leaves with the senescence rate being highest in February and lowest in July. The intrinsic fluctuation in tissue senescence rate might be caused by hormonal or other factors. Leaves growing during the long days in summer could contain higher amounts of senescence inhibiting regulators or lower amounts of senescence accelerating ones. No change in sensitivity to hormones was applied externally.

33. Based on the available evidence, neither a decline in endogenous levels of any currently known senescence-retarding hormone nor an increase in

a senescence promoter seems to be the primary event in the induction of senescence; however, such changes may well be part of, or contribute to, a more complex induction system (Thomas and Stoddart 1980).

34. Although often observed as yellowing of chloroplasts, senescence is usually initiated long before any symptoms are visible. Friedrych and Huffaker (1980) found that chlorophyll loss did not begin until 14 days after the initial loss of RuBPC. In detached leaves, senescence symptoms become clearly observable usually about 48 hr after leaf detachment. The senescence of leaves often involves loss of chlorophyll, increase in carotenoids, decline in protein and RNA levels, enhanced proteolysis, hydrolysis of starch and other polysaccharides, and, in some cases, increased respiration. Many different methods have been employed in measuring the rate of senescence. None of them seems to be applicable to all plants.

35. Manos and Goldthwaite (1975) suggested that the reciprocal of the time to 50-percent chlorophyll breakdown is a good measure of the rate of the overall senescence process in leaf tissues. Colquhoun and Hillman (1972) used RNA and protein assays for assessing the effect of ABA on senescence in leaf discs of radishes.

36. It is generally accepted that senescence follows flowering and fruiting. There might be cases when some stress-inducing factors cause an early senescence that influences flower initiation. This was described for *Lemna gibba* grown under controlled conditions by Kandeler et al. (1974). Duckweeds do not flower frequently in field conditions; they reproduce mainly vegetatively. However, flowering was often observed in dense stands of duckweeds that were exposed to extremely high temperatures and that might also suffer a nutrient deficiency. Shortly after flowering, whole stands usually died (Rejmankova 1973). It could be that the plants started to senesce because of stress conditions and that flowering was triggered by a change in the metabolism of the senescing plant.

Senescence and Disease

37. Disease of higher plants is more than just an act of parasitism; rather, it is a deleterious shift in the biochemical and physiological processes required for normal cellular function, differentiation, and reproduction (Daly and Knoche 1976). No matter how well the undamaged parts of an

infected plant compensate for the local effects of a pathogen, eventually the physiological control systems fail to function properly, and senescence and decay take over. Three areas can be identified wherein the pathogen may modify natural leaf senescence (Habeshaw 1984): (a) transport and sink effects between leaf and pathogen and leaf and plant, (b) the supply of nutrients, and (c) the effect of growth hormones. Very little is known regarding the nature of hormonal changes in diseased plants. In many cases it is not known whether hormonal imbalances in diseased tissues are the cause or the result of infection. In other words, does the plant senesce because it was attacked by the pathogen, or was it attacked by the pathogen because it was already in a senescent stage and therefore more susceptible to pathogen attack?

38. The long-term effect of attack by a parasitic fungus resulting in acceleration of senescence was described by Butler and Simon (1971). The view that certain microorganisms can benefit from the natural senescence of their host is supported by results of Kirk (1984). There is a general belief that weak pathogens are able to advance senescence (Smedegaard-Petersen 1985). The experimental evidence for this phenomenon is rather conflicting. In many cases, senescence in infected plants is accelerated by the reduction in the rate of photosynthesis brought about by toxic substances produced by pathogen (Krishnamani and Lakshmanan 1976).

39. It is clear that although a number of interesting approaches to the problem of senescence in plants are being taken, it is too early to be able to present a single, overall hypothesis that will account for all the facts. In general it can be recognized that the initiation of senescence involves a change in the relative levels of growth hormones, and this change in hormonal status may be caused by either internal factors or environmental stimuli.

40. There are apparently two types of senescence. One is the senescence that proceeds as a natural part of the whole plant development and is primarily controlled by internal genetic and correlative factors. The other can be called enforced or induced senescence (Butler and Simon 1971) and reflects the changes caused by some unfavorable environmental factors (mineral deficiencies, insufficient light) or diseases. The main focus herein is on the later aspect of senescence and its possible manipulation. Why is manipulation of senescence wanted? The potential benefits to be gained are in terms of

plant productivity (crop plants) if the senescence is delayed. For aquatic weed problems, however, it would be beneficial to accelerate senescence (selectively if possible) and thus make the weeds more susceptible to disease.

Senescence in Aquatic Plants

41. Except for a series of papers by Jana and Choudhuri (1979, 1980, 1981, 1982a-g, 1984) and Kar and Choudhuri (1985, 1986) describing senescence in detail in both intact and detached leaves of submersed macrophytes *Vallisneria spiralis*, *Hydrilla verticillata*, and *P. pectinatus*, there has not been much more published on senescence in aquatic plants. Senescence is briefly mentioned in several production-ecological studies; some data exist on translocation of minerals before and during senescence. Osborne (1984) in her review on the role of ethylene in aquatic and semi-aquatic plants briefly discusses the role of ethylene in senescence.

Results from outdoor ecological studies

42. Natural senescence is an integral part of the whole-plant development. Therefore the complete growth cycle of a plant must be understood for an understanding of natural senescence. The growth pattern of submersed macrophytes usually corresponds to the generalized pattern given by Westlake (1965). The typical curve is sigmoid, but finally the biomass starts to decrease (see Figure 2). In temperate and subtropical climates there is generally a rapid biomass increase in the spring, with the maximum in the summer. The maximum biomass usually occurs at the time of flowering. Occasionally there may be two distinct biomass maxima during the growing season. After flowering and formation of seeds, submersed aquatic species with an annual mode of growth gradually senesce (Adams and Prentki 1982, Brock et al. 1985, Kulshreshtha 1982, Ram and Kapoor 1976, Rogers and Breen 1980). Senescence of the below-ground parts in species with extensive rhizomes and roots (e.g., *Nympheaceae*) is usually a much slower process than the senescence of the above ground parts (Brock et al. 1985).

43. Many submersed macrophytes in temperate climates appear to grow as annuals. Some species always develop overwintering organs (turions) before they die (e.g., *P. pectinatus*, *Potamogeton natans*, *Vallisneria americana*); others persist without special perennation organs (*E. canadensis*, *C. demersum*); and some vary according to the local conditions (*Myriophyllum*,

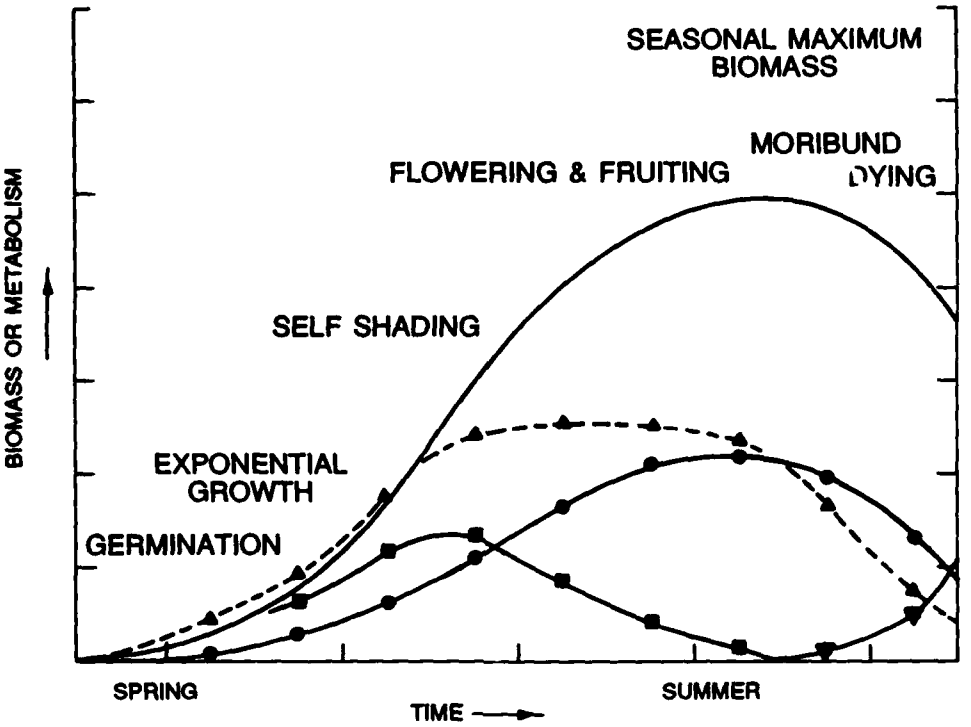

Figure 2. Hypothetical growth and metabolism curves for a plant with the annual mode of growth (———Biomass, - - -▲- - - current gross productivity, —■— current net productivity, —●— current respiration rate, —▼— death losses) (Westlake 1965)

H. verticillata). Carpenter (1980a), who studied nutrient release by three common macrophytes from Lake Wingra (*V. americana*, *M. spicatum*, and *P. pectinatus*), found that *P. pectinatus* senesces early in the season, while *V. americana* senesces late in the season. *Myriophyllum* shows more or less continuous leaching of organic material because there are always some senescent plants present in the population. The differentiated timing of the life cycle has been recognized as one of the strategies in sharing a habitat when niches are tightly packed. Another example of coexistence of several submersed macrophytes includes *Myriophyllum*, *Potamogeton*, and *C. demersum* (Crowder, Bristow, and King 1977).

44. Even if they are perennial, most of the submersed aquatic plants exhibit a typical annual mode of growth. They often produce special overwintering organs (turions, tubers, winter buds). The germination of these overwintering organs at the beginning of the growing season is usually very rapid. Nevertheless, these plants are still at a competitive disadvantage compared with those that overwinter in the form of the whole green shoots since the

latter are able to photosynthesize early in the spring. *Myriophyllum spicatum* is known to overwinter as a whole plant in many areas it invades. Its capacity for early growth at the beginning of the growing season is often cited as the reason for fast colonization and successful competition of native aquatic species.

45. Plants in northern temperate climates generally follow a unimodal pattern with a single growth maximum and relatively short periods of biological activity separated by a long period of inactivity due to severe winters. In warmer climates, a bimodal growth pattern prevails. This involves growth and maturation of two different age classes (overwintering shoots from the last year are usually responsible for the spring maximum, and new present-year shoots for the late summer maximum). Some plant species are apparently more flexible and are able to change their growth strategy in changing environmental conditions. Haag and Gorham (1977) and Haag (1979) give very instructive descriptions of different growth strategies of *Elodea, Myriophyllum*, and *Potamogeton* in Lake Wabamun in Alberta. They compare a part of the lake that freezes during the winter with a part receiving a thermal effluent. *Elodea* and *Myriophyllum* exhibit a rather flexible strategy compared with *Potamogeton*, which shows strong endogenous regulation of its growth. Two maxima were usually found for *M. spicatum* biomass in Lake Wingra during the years of its maximum spread. In 1977, when *M. spicatum* started to decline, there was only one maximum (Adams and Prentki 1982). Hannan and Dorris (1970) provide an interesting example of the development of submersed vegetation in natural conditions in a spring-fed river with almost constant water temperature as well as very uniform chemical composition. The macrophytes grew year-round with the gross photosynthesis dependent on light intensity.

46. There are not many studies on growth cycles and on the primary productivity of submersed macrophytes from tropical regions. Unni (1976) describes the production of several submersed species (*H. verticillata, C. demersum, Potamogeton crispus*, etc.) in a lake in central India. There are two distinct growth periods. The first one starts in January, and plants reach their maximum biomass in late March or April. The second growth period starts with the onset of rains in June, and the maximum biomass is reached by September. Following the maxima, some plants senesce and die, and some survive with a very slow growth till the following growth period starts.

47. Huebert and Gorham (1983), who studied the mineral nutrition of *P. pectinatus* under standardized environmental conditions, observed the striking seasonal periodicity in biomass production. They suggested that an internal seasonal regulation of the growth of *P. pectinatus* existed independent of obvious external environmental signals. Ram and Kapoor (1976) described this pattern in *C. demersum* grown from seeds: seed germination--differentiation--flowering--senescence, resulting in a sigmoid growth curve with the spread over a time period of 2 months.

Changes in mineral composition of plants during senescence

48. As the plant ages, it undergoes changes in its mineral composition. In perennials with underground storage organs, nutrients are translocated from below ground parts to the leaves at the beginning of the growing season. As the leaves senesce, the nutrients move in the opposite direction. Very often senescence appears to be induced in direct response to a deficiency, resulting in redistribution of the limiting nutrient from older tissue to developing structures such as young leaves and fruits. This is especially true for the mobile elements nitrogen, potassium, phosphorus, magnesium, sodium, and chlorine. Nutrients are not always translocated during senescence. In some species there is almost no translocation, and most nutrients are leached from disintegrating cells as senescence proceeds.

49. According to Prentki et al. (1978), 50 percent of the nutrients from senescent leaves of *Typha latifolia* are translocated into the below ground rhizomes. In eelgrass (*Z. marina*), both leaching and translocation are responsible for a decrease in total soluble organic matter, C and N in senescing leaves (Harrison and Mann 1975). As senescence started, there was only about one-third of nitrogen compared with the full-growth phase. Total organic matter dropped from 90 percent in young leaves to 28 percent in senescing leaves.

50. The changes in the contents of the main nutrients in *Phragmite* shoots during the growing season are summarized in Figure 3. The nitrogen content was highest in May, during the period of maximum growth. The sodium content reached a peak just before senescence and then fell sharply. The potassium content was highest at emergence and then fell steadily, with a sharp drop at senescence. Calcium levels increased to a peak in early July and then remained constant until senescence. The magnesium content remained

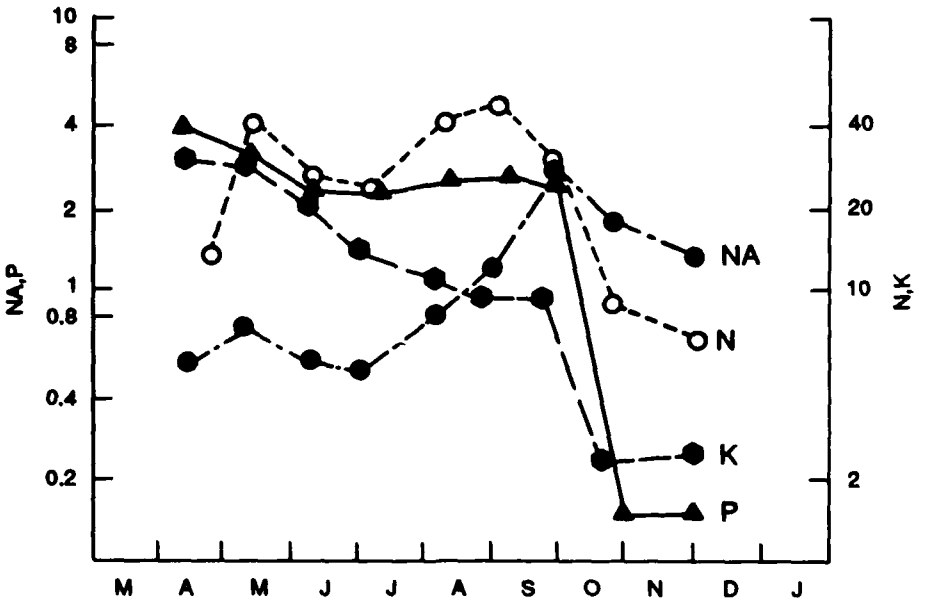

Figure 3. The amounts (mg/g^{-1}) of nitrogen (--○--), phosphorus (—▲—), sodium (-·●·-), and potassium (—●—) in shoots of *Phragmites communis* (Mason and Bryant 1975)

steady throughout. Many differences in the nutrient content of *Phragmites* and *Typha* can be detected (Boyd and Hess 1970, Kvet 1975, Dykyjova 1978), but the data shown in Figure 3 are reasonably representative for emergent macrophytes.

51. Typically, there is a seasonal decline in potassium content and then a sharper decrease during senescence. Besides emergent macrophytes, this pattern was also reported for submersed and floating species (Peverly 1985, Rogers and Breen 1980). High concentrations of potassium are required for the activity of many enzymes participating in intermediary metabolism and biosynthesis. Four main physiological and biochemical roles of potassium are recognized (Clarkson and Hanson 1980): (a) enzyme activation, (b) membrane transport process, (c) anion neutralization, and (d) osmotic potential. Barko and Smart (1981) hypothesized that lack of potassium might be a key element in triggering the senescence processes. Seasonal changes in chlorophyll content in several aquatic plant species followed a unimodal curve with a sharp decline corresponding to senescence (Ho 1979).

Induction of senescence in aquatic plants

52. Among environmental factors inducing senescence, temperature, light, day length, mineral nutrients, and heavy growth of epiphytes have most often been mentioned for aquatic plants, with sometimes conflicting evidence.

53. A decrease in water temperature was reported to induce senescence in *H. verticillata* and *Potamogeton berchtoldii*, resulting in abscision of winter buds and turions. However, in *P. crispus*, senescence was induced on *P. crispus* by increasing water temperature and day length (Sastroutomo 1982). Based on the results of experiments in greenhouse-heated tanks, Barko and Smart (1981) asserted that in *H. verticillata* and *Egeria densa*, higher temperatures accelerate senescence. Early senescence was observed in a dense stand of duckweeds, *L. gibba*, growing in a sheltered lagoon in a littoral of Nesyt Lake in Czechoslovakia (Rejmankova 1973). Water temperature was much higher in the lagoon than in the surrounding reedbelt where the duckweed grew more slowly but did not senesce until later in the growing season. Similar results were obtained for *L. gibba* growing in controlled conditions in the laboratory; life span was much shorter in conditions ensuring maximal growth as compared with the life span in less favorable conditions (Rejmankova 1979). Apparently, temperatures providing maximal growth also advance the onset of senescence. Comparison of growth of *M. spicatum* in a cooling reservoir at three locations with different water temperature showed differences in phenological advancement (Grace and Tilly 1976). The warmer the temperature, the more advanced phenology, which results in the earlier senescence.

54. Submersed aquatic plants are usually well adapted to low light intensities. Once the light intensity decreases under the compensation point, plants start showing symptoms of senescence. One of the reasons for decreasing light intensities is higher water turbidity caused by either anorganic silt particles or phytoplankton blooms (Spence 1972). A sudden increase in water turbidity occurred in Cayuga Lake in 1972 as a consequence of tropical storm Agnes (Oglesby and Vogel 1976). In some plant species, a temporary submergence in the dark does not induce senescence but only quiescence (i.e., a temporary suspension of growth). Quiescence can be immediately relieved by transfer from dark to light, as was shown experimentally by Quimby and Kay (1977) for alligatorweed.

55. High light intensities are also known to be responsible for early senescence, especially in plants previously adapted to low light, as shown under experimental conditions by Barko and Smart (1981).

56. In some plant species, the day length changes seem to be important in inducing senescence. Drew (1979) reported the summer reduction in chlorophyll content in a seagrass *Posidenia* as a sign of senescence induced by changes in the photoperiod. Spencer and Anderson (1986a) recorded a decrease in chlorophyll *a* and carotenoid content in *Potamogeton nodosus* after the switch from long-day to short-day conditions. *Potamogeton pectinatus* did not display similar changes (Spencer and Anderson 1986b).

57. There are reports on the shading effect of epiphytic algae causing the early decline of submersed macrophytes (Kiorboe 1980b, Adams and Prentki 1982). Kiorboe (1980b) compared the seasonal increase of the biomass of *M. spicatum, P. pectinatus*, and several other submersed species from two different localities in a fjord in Denmark. At one locality, all macrophytes except for the *Chara* were heavily overgrown with epiphytes. These plants had almost half as much biomass and started to senesce about 1 to 2 months sooner compared with those without epiphytes. The heavy growth of epiphytic microorganisms was reported as being responsible for early senescence in *P. crispus* (Rogers and Breen 1981).

58. Mulligan et al. (1976) fertilized small experimental ponds containing submersed macrophytes (*E. canadensis, M. spicatum, Chara*) with nitrogen and phosphorus. They found that except for *Elodea*, the other species were not able to grow in the heavily fertilized ponds but senesced and died. It is questionable whether the main reason for the macrophyte decline was too high a concentration of nutrients or a heavy phytoplankton bloom responsible for increased light attenuation.

59. Herbicides in sublethal concentrations may enhance senescence in aquatic plants. Even if most herbicide tests are oriented towards finding lethal doses, there are some papers describing sublethal concentrations (Fowler 1977), especially in combination with other types of control (Charudattan 1986).

Senescence and turion production

60. Some aquatic plants produce specialized buds that are important both in vegetative reproduction and in the survival of the species through periods of stress (e.g., winter in the north temperate regions). Several different

terms have been used for these buds such as winter-buds, turions, hibernacula, and resting buds. These vegetative propagules have lately received a lot of attention, namely in *Hydrilla* and *Myriophyllum*. The objective has been to define the conditions under which they are produced (Weber and Nooden 1974, 1976; Aiken and Walz 1979) and to find ways to prevent or limit their production (Klaine and Ward 1984, Spencer and Anderson 1986a). In *Hydrilla*, vegetative propagule production is stimulated by a shortened photoperiod and does not seem to be temperature dependent. Artificial illumination during the night prevents propagule formation. A short-day photoperiod enhanced vegetative propagule production in *P. pectinatus* and *P. nodosus* (Spencer and Anderson 1986b).

61. In *Myriophyllum verticillatum*, turion development is controlled by both photoperiod and temperature. Weber and Nooden (1974) noted that detached shoots form turions earlier than rooted plants. The effect of detachment could be a response to mineral nutrient deficiency in water. Rooted plants which absorb most phosphorus and nitrogen from the substrate that does not undergo any substantial seasonal changes in nutrient amount compared with water are not expected to have their turion formation induced by nutrient deficiency. After abscission of turions and after formation of tubers in *Hydrilla*, the vegetative shoots usually senesce and die. There is not always abscission of the propagules from the vegetative plant. *Myriophyllum exalbescens* turions differ from those of *M. verticillatum* in size and shape, but the main difference is that there is no abscission layer at the base of *M. exalbescens* turions. As the turions become heavier during the winter, they sink to the bottom with the senescent pieces of parent plants still attached (Aiken and Walz 1979). Not much is known about what happens with the vegetative shoots if they are prevented from forming turions.

Senescence studied on detached leaves of submersed aquatic plants

62. Plant physiologists studying senescence are usually interested in a very narrow part of the whole process (e.g., the behavior of a single organelle or a specific enzyme). The test plant or leaf is chosen according to its suitability for that special type of research without consideration of reactions of the whole plant population in its natural environment.

63. One of the first senescence studies in which an aquatic plant was used as a test object was done by Yoshida (1961, 1970), who studied

chloroplast senescence in detached leaves of *Elodea densa*. Yoshida indicated that chloroplast senescence is closely associated with the nucleus. Makovetzki and Goldschmidt (1976) continued chloroplast senescence studies using detached leaves of *E. canadensis*. Their conclusions confirmed that chlorophyll senescence is under nuclear/cytoplasmatic control, and chloroplastic proteins synthesis is not required for chloroplast senescence.

64. A series of papers has been published on the senescence phenomenon in aquatic macrophytes (*H. verticillata, V. spiralis,* and *P. pectinatus*) by Indian scientists Jana and Choudhuri (1980, 1981, 1982a-g, 1984) and Kar and Choudhuri (1985, 1986). The authors used mostly detached leaves for their experiments and occasionally compared their results with data on intact leaves. Even if one may doubt the direct applicability of results obtained on detached leaves to intact leaves/plants, these results still serve as an indication of possible changes that can be expected during senescence.

65. In their first paper on senescence Jana and Choudhuri (1980) compared the protein and chlorophyll content as well as enzyme activities in young, mature, and old leaves of *Vallisneria* and *Hydrilla*. Later, the same tests were repeated with *P. pectinatus* (Jana and Choudhuri 1982g). In all plants, the amount of chlorophyll and protein content was highest in mature leaves, lower in young leaves, and lowest in the old leaves. Protease and RNase showed increasing tendencies from young to old leaves; catalase activity decreased. Contrasting results were obtained with acid and alkaline pyrophosphatases; both decreased with leaf age in *Hydrilla* while they increased with age in *Vallisneria* and *Potamogeton*. In detached leaves, the enzyme behavior was not the same as in intact leaves. Kinetin in all concentrations tested was effective in delaying senescence in detached leaves. The concentration of 50 µg/mℓ was the most effective. When comparing the metabolic decline due to aging in tested plants, the authors concluded that the decline in *Hydrilla* was slower than in *Vallisneria* and *Potamogeton*.

66. Jana and Choudhuri (1982a) also studied glycolate metabolism in the above-mentioned plant species. Glycolate (which is the substrate of photooxidation and the key enzyme of this process) and the glycolate oxidase were measured in different age groups of leaves and in detached leaves. Both glycolate content and enzyme activity were highest in mature leaves and decreased with aging. The activity of RuBP carboxylase also decreased with the onset of

senescence (Jana and Choudhuri 1982d), which is in agreement with results for terrestrial plant species (Friedrych and Huffaker 1980).

67. All three tested plants were found to produce an increasing amount of ethylene with aging (Jana and Choudhuri 1982e). Ethylene is known to be involved in the senescence of terrestrial plants. Production of ethylene was reduced by kinetin and enhanced by ABA in all three species.

68. In other experiments (Jana and Choudhuri 1981, 1982c, 1984), *Hydrilla* was more tolerant to heavy metals (mercury, cadmium, copper, and palladium) than were *Potamogeton* and *Vallisneria*. All tested heavy metals apparently hastened the onset of senescence, possibly, as the authors suggested, by impairing the general synthetic ability and membrane integrity of tissues of treated plants. Kar and Choudhuri (1985, 1986) measured senescence characteristics in detached leaves in light and darkness and following treatment with the polyamine spermine.

69. Strother (1984) measured the activities of acid and alkaline pyrophosphatases in senescing duckweeds, *Lemna minor*, grown in either complete or phosphorus deficient medium. Alkaline pyrophosphatase is supposed to be an enzyme most active in the conditions of highest metabolic activity. Acid pyrophosphatase has a role of phosphate scavenger and helps to maintain phosphate homeostasis. In *L. minor*, the activity of alkaline pyrophosphatase decreases during normal senescence; its decrease is accelerated by phosphorus deficiency. Acid phosphatase activity increases slightly during senescence. Under phosphorus deficiency, its increase is higher.

Senescence versus decomposition

70. Decomposition (decay) is a process immediately following senescence. It is defined as a degradation (usually microbial) of dead organic material. It is not always easy to distinguish between senescence and decomposition. Part of a leaf may be already dead and decomposing while the rest is still senescing. The distinction between senescing and decomposing plants or their parts is often somewhat arbitrary.

71. A continuum of certain symptoms is also typical for both processes. Organic matter is being released by senescing cells and continues to be released, more rapidly, after these cells die. Often the same microorganisms are present on senescing as on dead plants; their numbers and activities increase on dead plants. In most plant production, senescence and decomposition follow sequentially in any organ and may occur simultaneously during the

life span of a plant as older organs (particularly leaves) die, and new ones are produced (Rogers and Breen 1982). In a population, some plants will begin to senesce and decompose earlier than others. A good understanding of natural senescence and decomposition processes within the population of aquatic plants is, by all means, necessary for any attempts to manipulate these processes from outside.

72. Knowledge of the decomposition processes, especially of the rates of decomposition, is essential to an understanding of the role macrophytes play in aquatic ecosystems. Consequently, numerous studies describing decomposition of different aquatic plants have been published (Solski 1962; Nichols and Keeney 1973; Mason and Bryant 1975; Kistritz 1978; Karpati and Pomogyi 1979; Carpenter 1980a; Adams and Prentki 1982; Polunin 1984; Brock et al. 1985). The most commonly used method for studying decomposition is the so-called "litterbag technique," which involves the use of nylon bags filled with cut pieces of a plant. The bags are placed in water, and in successive intervals changes in dry weight and, occasionally, nutrients are measured. Unfortunately, in many litterbag experiments, healthy plants that had been previously killed (mostly by drying in the oven at 105° C or by freeze-drying) were used as an initial material for decomposition, which makes the results hardly comparable with natural field conditions.

73. Kudryavstev and Kudryavsteva (1980) compared dry weight loss during decomposition in *Potamogeton lucens* samples collected in different stages of its development. Samples originating from young healthy plants were found to have a much higher initial loss of dry weight than samples from already senescing plants. Similar results were obtained by Rogers and Breen (1982) with *P. crispus*. They compared decomposition, measured as the loss of weight and main nutrients, of naturally senescent plant material with that obtained when plants were artificially killed by drying. The authors found that the overall rate of weight loss from dried plants was slower than that of senescent plants even if the initial loss was more rapid for the dried plants. Howard-Williams and Davies (1978) measured the rates of dry matter and nutrient loss during decomposition of *P. pectinatus*. They used *P. pectinatus* shoots in a late senescent stage as an initial material for litterbag tests, and they even gradually shifted the bags down in the water column so as to simulate the conditions in a natural dying *P. pectinatus* stand.

74. The decomposition process can be generally described by an exponential curve (Best et al. 1982, Rejmankova 1979). The more detailed studies often point out that during the first days, the decomposition proceeds much faster than the predicted exponential curve. The initial deviation is most certainly caused by the physical effects of leaching. The decomposition rate is dependent on the type of plant material used for decomposition. The half times of decomposition vary between 200 to 400 days for emergent macrophytes (*Typha, Phragmites*) and are much shorter for floating and submersed macrophytes (*Lemna, Nymphaea, Myriophyllum, Potamogeton*), usually between 20 and 50 days. The rate of decomposition also depends on temperature; it was found to decrease exponentially with decreasing temperature (Rejmankova 1979).

75. Godshalk and Wetzel (1978) followed the fate of dissolved organic compounds (DOM) released from senescing and decomposing aquatic plants. The rate of metabolism of these compounds was dependent on temperature but mostly on the oxygen content of the water. In oxygen deficient waters, DOM accumulates, while in oxygen-rich waters, the metabolization to CO_2 is very efficient. A model to predict daily release of DOM and dissolved total phosphorus from three decomposing species (*M. spicatum, V. americana,* and *P. pectinatus*) in Lake Wingra was constructed by Carpenter (1980a). Sterry et al. (1985) described the major end products of microbial decomposition of two aquatic species (*C. demersum* and *Lemna pucicostata*) in a closed system after 42 days. Despite differences in their morphologies, habitats, and epiphytic flora, the decomposition in both species led to the same products: acetate, propanoate, butanoate, and hydrogen. The absence of methane indicated nonmethanogenic fermentation. The plants were allowed to decompose in an oxygenated system with the microorganisms originally present in their phyllospheres. The methanogenic bacteria that require a completely anoxic environment were unlikely to be present, which explains why fermentation did not proceed beyond the acid-forming phase.

PART III: MICROORGANISMS ON AQUATIC PLANTS

76. All microscopic plants and animals should be regarded as microorganisms, i.e., bacteria, fungi, unicellular algae, protozoa, and the smallest metazoa. Also, viruses are included in the group of microorganisms even if they are not independent organisms themselves. Microorganisms play a very important role in aquatic ecosystems. This review is mainly focused on those aquatic microorganisms that are growing on or attached to aquatic plants and are capable of damaging these plants either directly (pathogens) or indirectly (light limitation, physical damage).

77. There are several ways in which plant pathogens exert stress or influence on their host plants. They can produce enzymes that dissolve the cell wall (cellulose, pectinase activities) or produce surface-bound and extracellular polysaccharides, toxins, or phytohormones. Bacterial phytotoxins were reviewed by Strobel (1977). The genetics of pathogenicity and selected aspects of molecular biology of microbial pathogens were reviewed by Panopoulos and Peet (1985). Only a few papers from the vast amount of literature on plant pathogens deal with aquatic plant pathogens (Zettler and Freemen 1972, Andrews 1980).

Interactions Between Epiphytic Microorganisms and Their Macrophyte Hosts

78. Many aquatic bacteria, fungi, or unicellular algae live within or on the surface of higher aquatic plants. The attached microorganisms are called "epiphytic" (epiphytes, epiphyton, periphyton--for details on terminology, see Appendix A (Glossary) and Sladeckova (1962)). They may use plants just as a physical support, or they may be commensals and derive all or some of their food from the food or metabolic products of their hosts. Generally, this does not involve any advantages or substantial disadvantages for their hosts. There are, however, other microorganisms that, as parasites, feed on the cells of their host, often producing toxic substances and thereby causing disease and often death. These are the pathogenic microorganisms. The distinction between commensalistic and parasitic microorganisms is not always very clear. Often fungi or bacteria may be present on a macrophyte for a long time without causing any symptoms in the plant and then may become parasitic when the

macrophyte is stressed when it is in a senescent stage. The term "opportunistic" is often used to describe this behavior. The term "saprophyte" is usually meant as an opposite to parasite, but because saprophyte refers strictly to organisms obtaining nutrients from dead organic material, one should use the term "commensals" for those epiphytic microorganisms feeding on dissolved organic matter excreted by their living hosts.

79. Microbial epiphytes have a variety of physiological relationships with their host plants. Besides being able to become pathogenic themselves, they can, on the other hand, reduce the inoculum potential of a pathogen either by simply occupying the area invaded by the pathogen or by producing antibiotics against the pathogen (Leben 1965, Blakeman 1971).

80. Most pathogens of aquatic plants contact their host passively with the aid of water. No chemotactic responses have been reported. To infect a plant, pathogens must penetrate a physical barrier (the cuticle and the cell wall of the plant). Most pathogenic bacteria and some pathogenic fungi enter their host passively through natural openings (wounds, stomata), but some have evolved sophisticated means for active penetration (Misaghi 1982).

81. There are many descriptive papers on epiphytic organisms, primarily algae, in aquatic ecosystems. They deal mainly with species composition (Jones and Mayer 1983), spatial and temporal distribution (Bowker and Denny 1980, Goldsborough and Robinson 1985, Stowe 1982, and others), and biomass production (Bulthuis and Woelkerling 1983, Howard-Williams and Liport 1980, Penhale 1977, and others) of periphyton. Many studies that were done on periphyton did not even consider a host plant as an important part of a microorganism-macrophyte complex and used artificial substrata for evaluation of periphyton growth (Cattaneo and Kalff 1978).

82. Much less information is available on the physiology, nutrition, energetics, or pathogenicity of epiphytes in an aquatic ecosystem and on actual interactions between macrophyte and attached microorganisms. Some macrophytes do not have periphyton because of the release of compounds toxic to algae, (e.g., as described by Anthoni et al. (1980). More commonly, however, dense and productive periphyton communities of algae and bacteria, often embedded in a carbonate muco-organic complex, develop on most macrophytes. Shading and nutrient depletion at the leaf surface are the major effects on the macrophytes. Heterotrophic microorganisms and algae can use dissolved organic carbon released by the macrophyte. The metabolic activity of the

heterotrophs, in turn, promotes the growth of algae and, probably, of the macrophyte by increasing the rate of mineral cycling (Sondergaard 1983). Pip and Robinson (1982) stressed the importance of the physical arrangement of epiphytic organisms and their host relative to each other.

83. Figure 4 shows interactions between macrophytes and their epiphytes. A very thorough study on primary productivity, chemoorganotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral region of a small temperate lake was done by Allen (1971). Allen's results confirm that DOM released extracellularly by macrophytes is rapidly incorporated into the epiphytic complex. Based on a series of experiments with axenic bacterial, algal, and macrophyte (*Najas flexilis*) cultures, Allen showed that organic materials released by *Najas* were not wholly suitable as carbon and energy substrate for algae without prior bacterial degradation. Allen also described how the colonization of a macrophyte proceeds. During initial colonization, bacteria adhere and probably form a monocellular layer. This is subsequently infiltrated with calcium carbonate precipitated by the macrophyte and algal forms, particularly in calcareous waters. As colonization intensifies (late spring and early summer), a dissolved organic carbon "pool" is probably established in the matrix of deposited carbonates. Its

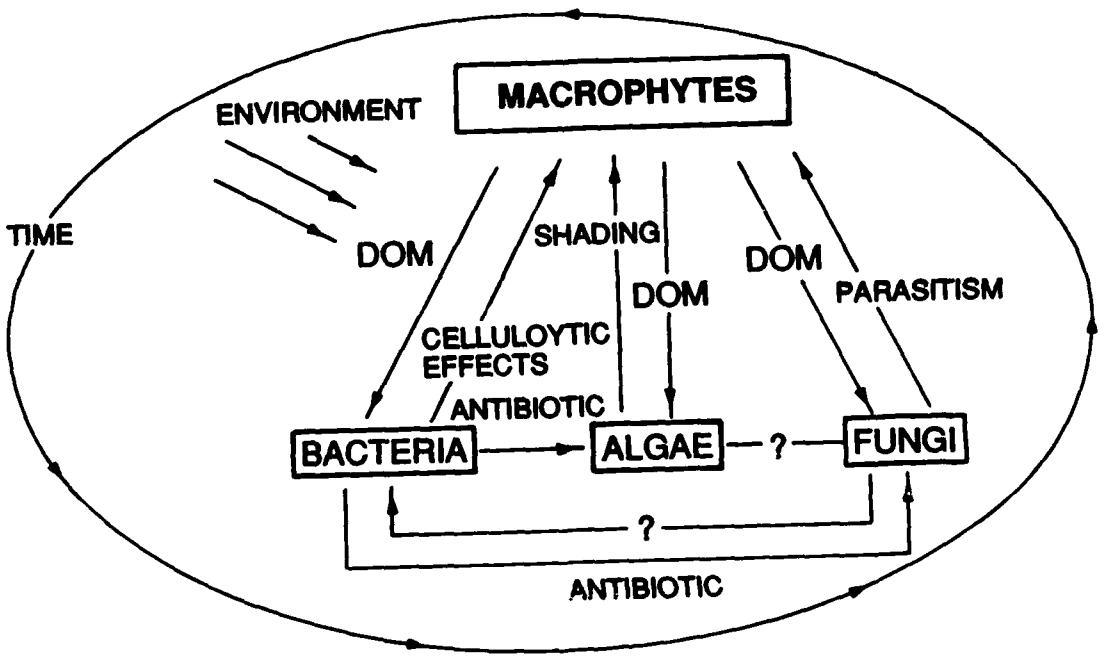

Figure 4. Generalized pattern of interactions in a macrophyte-epiphytic microflora complex

sources are: (a) extracellular release from macrophytes, (b) active excretion from attached algae and bacteria, (c) decomposition products following autolysis of epiphytes, and (d) dissolved carbon compounds present in littoral water. Wetzel and Allen (1970) suggested a metabolic model of macrophyte-periphyton interactions. Its validity was confirmed by Allanson (1973), who studied the periphyton structure on *Potamogeton natans* and *Chara*. The relationships between epiphytic microfloral populations and the substrata upon which they grow were reviewed by Wetzel (1983). He admits that much is still unknown, and he stresses that in situ metabolism at the microlevel must be analyzed as well as quantification of the metabolic pathways by direct experimental methods.

84. A microcosm consisting of several types of microorganisms was described in internodal areas of *Spartina alterniflora* (Gessner et al. 1972). At first, fungal mycelia of *Sphaerulina pedicellata* with characteristic hyphopodia develop on the surface of growing Spartina. Hyphopodia serve for attachment, penetration, and absorption. As the fungal biomass increases, additional microorganisms appear, namely bacteria, such as *Metallogenium*, *Hyphomicrobium*, and *Mycoplasma*. These bacteria are known to grow only in the presence of fungi. The occurrence of the nematodes of *Oncholaimus* among the fungal mycelium as well as the presence of acarid mites is typical. During the senescence of *Spartina*, the fungal growth accelerates.

Bacteria

85. As was the case for other epiphytes, epiphytic bacteria have been the subject of mainly descriptive studies. Bacteria have been enumerated and occasionally their biomass estimated, but not much is known about their functions and interactions with host plants. They are regarded as initial colonizers of aquatic plants using organic matter exuded from macrophytes or released by aphid or other insect action from subcuticular tissues (Lee 1980). However, the evidence of the sequence of microfloral succession on aquatic plant material has been controversial (Robb et al. 1979). Many earlier studies regarded fungi as primary colonizers on decaying plants (Gessner et al. 1972).

86. The density of epiphytic bacterial populations in aquatic ecosystems depends on various factors. It tends to increase as a result of bacterial attachment and growth whereas expansion of plant tissue, detachment of bacteria, predation, and death can cause a decrease. Hossell and Baker (1979a, b) estimated average bacterial numbers on the lower surface of *Lemna minor* leaves and on *Rorippa* leaves. They found that bacterial density increased significantly with leaf age. Patience et al. (1983), who studied the decomposition of *L. paucicostata*, provided evidence that the microorganisms involved in decomposition are mainly rod-shaped or coccoid bacteria which are present in high densities on the lower surfaces of living *Lemna* leaves. Spatial distribution of epiphytic bacteria on seven species of aquatic plants was described by Baker and Orr (1986). The authors confirmed that the older leaves have much higher bacterial density. Two investigated species (*Nasturtium officinale* and *Veronica beccabunga*) were found to have significantly larger populations on the abaxial surfaces of submerged leaves than on the adaxial surfaces. The difference may be due to the unilateral release of hydroxyl ions during bicarbonate utilization.

87. Rhizosphere bacterioflora of *L. minor* was described by Coler and Gunner (1969); that of *Myriophyllum heterophyllum* by Blotnick et al. (1980). Both papers confirmed that microbial activity is enhanced by exudation of organic substances from aquatic plants. Density and production estimations of bacteria on several macrophyte species were presented by Kudryavstev (1984) and Kudryavstev and Yeshov (1980). They found increasing numbers of cellulolytic bacteria from the spring to the fall. Among the macrophyte studied, pondweed (*Potamogeton*) had the most abundant bacterial epiphytes.

88. Rogers and Breen (1981) studied the epiphyton colonization of the leaves of *P. crispus* and tried to establish its effect on the host plant. They did not find any differences in colonization of abaxial and adaxial surfaces of the leaves. The youngest leaves were devoid of epiphyton. The young leaves were colonized by groups of short stout bacteria that appeared to be attached to the leaf surface by weblike structures. With increasing leaf age, the epiphyton became denser and included a greater variety of species. Besides short stout bacteria, some cyanobacteria were present as well as some bacilli and several diatoms species. The oldest leaves did not show any changes in species diversity, but the epiphyton increased in density. The electron microscopy revealed that bacterial attachment did not damage the

surface of young leaves. There were, however, extensive inward swelling and disorganization of the epidermal walls, characteristic of a reaction to invasion by pathogens. In older leaves, the swelling was also present in mesophyll cells while bacteria had invaded and degraded the epidermal cell wall. The bacterial invasion was concomitant with signs of senescence.

89. In a later study, Rogers and Breen (1983) included grazer interaction in their studies. The host plant (*P. crispus*) was resistant to consumption by snails until it was invaded by epiphytic necrotrophic bacteria, which made the host tissue more palatable for the grazer. Grazing of epiphytes by the snails, however, reduced the rate of development of the bacteria and probably extended the life of the plants. A succession of microflora on developing leaves of *P. pectinatus* was examined by Howard-Williams and Davies (1978). They found that prosthecae bacteria developed after 6 weeks of leaf growth. These bacteria were associated with cuticular erosion and epidermal pitting. Several weeks later the senescing leaves showed extensive cuticular peeling and epidermal cell wall rupture. Details of the forms of bacterial attachment to leaf surfaces of *P. pectinatus* were described by Robb et al. (1979). The authors assayed individual isolate cultures for cellulase activity and found that six out of eight isolates produced extracellular cellulase.

90. Bacterial attachment proceeds in the following stages: (a) a reversible ionic attraction, (b) secretion of an adhesive acidic polysaccharide that develops either into a fibrous web or a network of fimbriae, and (c) the formation of clumps. These steps seem to be necessary morphological adaptations in an aquatic environment; they allow for concentration of exoenzyme activity on a food substrate. Adhesion-enhancing materials and their specificity for bacteria-host interactions were described by Imam et al. (1984). It is generally believed that the entry of bacteria into plants requires wounds because epidermal cell walls are protected by cuticle (Kolattukudy 1985). The above examples show that this is not always the case in aquatic plants, presumably because the cuticle in submerged macrophytes is extremely thin and reduced (Sculthorpe 1967).

91. Many papers describe the epiphytic microflora on seagrasses. Kirchman (1984) measured dissolved organic carbon excretion rates by *Z. marina* leaves. It equaled 2 percent of total carbon fixation, and the epiphytic bacterial population was supported almost entirely by carbon obtained directly

from *Zostera* photosynthesis. Bacterial colonization was much higher at the tips of the leaves (*Zostera* leaves grow at the base, which means that leaf tips are older). The doubling time for bacterial population was 8 days. According to Waite and Mitchell (1976), the bacteria living on the surface of *Ulva lactuca* leaves act as typical opportunists. Under normal conditions they provide essential growth factors for their host, but they are capable of degrading *Ulva*. The degradation process is presumably triggered when *Ulva* gets into stress conditions. Lemos et al. (1985) isolated 224 bacterial strains from marine green and brown algae; 38 of these strains, all from the *Pseudomonas-Alteromonas* group, displayed antibiotic activity.

92. Waite and Kurucz (1977) isolated bacteria from decaying *Hydrilla* plants and tested them for the ability to produce cellulolytic enzymes. Those isolates able to degrade cellulose were used as inoculum for the degradation of *Hydrilla*. The plant material was autoclaved prior to inoculation, and the kinetics of plant material degradation was measured.

93. In recent years, attempts have been made to use epiphytic microorganisms to produce lytic enzymes for potential control of nuisance aquatic weeds. Gunner (1983) studied cellulolytic properties of enzymes produced by microorganisms occurring naturally on the surface of watermilfoil species. The principal microflora was bacterial. The author tested individual isolates as well as their mixtures and concluded that a mixture of microbial isolates was more effective in attacking the plant than the isolates individually. Pennington (1985) conducted a search for microorganisms among endogenous microflora of hydrilla that would be able to increase their production of lytic enzymes and hence be able to attack plant tissues. She did not find any cellulase bacteria and only one pectinase-producing bacteria isolate.

94. Ramsay and Fry (1976) and Fry and Ramsay (1977) studied the response of epiphytic bacteria from the treatment of *E. canadensis* and *Chara vulgaris* with the herbicide paraquat. The number of epiphytes on *Chara* that was resistant to paraquat did not change after the treatment. Epiphytes on *Elodea* that died after 15 days following the treatment had all increased in number in the following 10 days; apparently their growth was stimulated by the soluble organic matter released from dying *Elodea*. The difference in the number of epiphytes before and after the treatment was greater for *Elodea* plants that were healthy prior to the treatment compared with those that were initially moribund.

95. Table 1 gives several examples of bacteria described from aquatic plants. Many so-called "low-grade" phytopathogens are among bacteria. These phytopathogens usually attack plants that are under stress. Several *Pseudomonas* species belong to these low-grade phytopathogens. Several examples of *Pseudomonas* isolated from different aquatic plants are shown in the table.

Epiphytic Algae

96. Numerous papers have been published on algal epiphyton, but most of them have paid little attention to the substrate. On the other hand, many studies of aquatic plants note the presence of epiphyton without going into any details. Complex studies involving both epiphytic algae and their host macrophyte are scarce, especially those that evaluate what changes occur in a macrophyte as a consequence of periphyton colonization.

97. Periphyton studies are often complicated by methodological problems arising when periphyton has to be removed from its substratum. A review of methods of periphyton measurements was prepared by Weitzel (1979). An up-to-date evaluation of suitable methods and techniques has been presented by Delbecque (1985), who commented on the many different techniques used from simple shaking or scraping the host plant free of its periphyton to complicated bleaching techniques or enzymatic removal of particularly prostrate species. Apparently each approach requires a special technique, and one solution for all problems cannot be given. Carter (1982) described a technique for direct microscopic observation of periphyton on macrophytes. Another controversial issue is how to express the amount of periphyton. Many authors try to relate the periphyton biomass to the unit of leaf surface area of the host. In species like *Myriophyllum* or some *Potamogeton*, the leaf morphology is so complicated that determinations of average surface areas can usually be only a rough estimate. Therefore, expressing the periphyton amounts in terms of dry weight of macrophyte hosts seems to be less erroneous (Gough and Woelkerling 1976).

98. A common practice in studies of epiphytic communities is the use of artificial substrata. Seasonal changes in the epiphyton community on natural macrophytes (*Potamogeton richardsonii*) and on a similar plastic plant were compared by Cattaneo and Kalff (1978). The authors concluded that there were no significant differences in community composition in the early season; the

differences that developed subsequently appeared to be principally a function of the amount of $CaCO_3$ incrustation. In their further study, Cattaneo and Kalff (1980) evaluated the relative contribution of macrophytes and their epiphytes to the total production. *Myriophyllum spicatum*, *P. richardsonii*, and *V. americana* were compared and, again, artificial plants were used as well as natural ones. *Myriophyllum*, a species with the most highly dissected leaves, supported greater epiphyte biomass than the other plants. Cattaneo and Kalff (1978, 1980), as well as Fontaine and Nigh (1983), were convinced that over most of the growing season, macrophyte hosts serve as a neutral substratum for their respective epiphytes. Only during periods of macrophyte senescence caused by metabolite leakage may macrophytes become relatively more important in structuring epiphyte communities.

99. In strong opposition against the "neutral substrate" theory are O'Neil, Morin, and Kimball (1983) and Wetzel (1983), who argue that by placement of the artificial substrata used in the above-mentioned studies in situ in the macrophyte stands, periphyton colonizing the artificial substrata was exposed to macrophyte-induced changes in the surrounding aquatic environment.

100. Many algal epiphyton studies deal exclusively with diatoms that often are a major contributor to an epiphytic community. Stowe (1982) described the development of the diatom community on *S. alterniflora*. The maximum diatom numbers occurred during the period of *Spartina* standing crop decline. Leachates released from dying grasses apparently provided nutrient stimulation for diatom growth. Seasonal succession of diatom epiphyton on *L. minor* was studied by Goldsborough and Robinson (1985). Maximum diatom biomass was recorded in early spring while the diversity reached its maximum during the decline of duckweed biomass. The extensive bloom of diatoms on decomposing *M. spicatum* under the ice in Lake Wingra was reported by Boylen and Brock (1974). A distribution of epiphytic diatoms on the lower side of leaves of *Nuphar lutea* and *Nymphoides alba* was described by Delbecque (1983). No differences in diatom colonization were found between the two nymphaeid species.

101. Macrophyte-mediated changes in the abundance of algal epiphyton were described by O'Neil, Morin, and Kimball (1983) for epiphyton on *M. heterophyllum*. The dense growth of *Myriophyllum* influenced physical and chemical conditions in the surrounding water column. Periphyton was dominated by diatoms in the early summer when the macrophyte occupied only the lower part of the water column. By midsummer the entire water column was occupied by

M. heterophyllum whose metabolic and photosynthetic activity and dense foliage created marked vertical gradients in physicochemical conditions. Periphyton species composition shifted to blue-green and filamentous algae on the apex and midstem. On the lower stem, diatoms consistently dominated the periphyton. Spring diatom maximum followed by a dominance of blue-green and filamentous algae in summer was also reported by Marvan et al. (1978).

102. Numerous papers describe algal epiphytes on brackish and marine submersed macrophytes. As these macrophytes are important as the primary producers in shallow tropical and temperate regions, they have been a subject of many production ecological studies (Harlin 1973, 1975; Ballantine and Almodovar 1977; Penhale 1977; Congdon and McComb 1979; Jacobs and Noten 1980; Willcocks 1982; Bulthuis and Woelkerling 1983; Moriarty et al. 1985; and others). Most of these authors agree that epiphyte colonization is heaviest on the oldest parts of leaves. Howard-Williams and Liport (1980) found very high epiphyte biomass on leaves of *Zostera*, often exceeding the biomass of the leaf itself. The role of epiphytes in the primary productivity of *Zostera muellri* in Westport Bay, Australia, was described by Clough and Attiwill (1980); the epiphytes themselves contribute to the biomass production, but at the same time, they shade their host plant, thus apparently lowering its photosynthesis. Heijs (1985a) measured the biomass contribution by epiphytes to be as high as 35 to 44 percent of the total aboveground production. According to Verhoeven (1980), the shading of epiphytes does not really suppress the macrophyte photosynthesis substantially because the most dense epiphyton develops on the older leaves that are not so much photosynthetically active anymore. Johnstone (1979) found that epiphyte colonization restricts the photosynthetically active life of a leaf segment to less than 25 days. Sometimes grazing can contribute to the regulation of epiphyton growth and to maintaining the viability of seagrasses (Van Montfrans et al. 1982).

103. The importance of epiphytic algae in nutrient cycling (especially phosphorus and nitrogen) was described by Allen (1971) and Mickle and Wetzel (1978). Riber at al. (1983) pointed out that a considerable proportion of the phosphorous pool of a lake passes through the algal periphyton during the year. Many authors also reported on the excretion of organic carbon and its subsequent utilization by epiphytes (Wetzel and Penhale 1979).

104. Physical and chemical parameters regulating growth of algal epiphytic communities were discussed by Sand-Jensen (1983). The author

stressed that while the physicochemical parameters above the epiphytic community can be measured reasonably well, the conditions within the community are often quite different. This is true particularly for thick and dense epiphyton communities in standing waters. Nevertheless, simple measurements can be done relating the physical (light, temperature) and chemical (inorganic nutrients) factors to the composition and biomass of epiphytic algae.

105. The epiphytes are capable of reducing the photosynthetic rate of their host by reducing the light intensity (Penhale 1977). Sand-Jensen (1977) measured the light intensity reduction of about 45 percent by a thick crust of epiphytes, mainly diatoms. In a further study, he measured that in a lake with a high nutrient supply, epiphytes were responsible for 86 percent of light attenuation. Selective light attenuation by the periphyton complex was characterized by Losee and Wetzel (1983). Debusk and Ryther (1981) observed lowering in the productivity in unharvested cultures of *H. verticillata*. They explained it as a result of severe light limitation on a dense *Hydrilla* mat. They noted an extensive epiphyton growth that was also apparently responsible for restricted growth.

106. Several examples have been described where epiphyton was so heavy that it actually dragged down and submerged aerial shoots of submersed macrophyte species (Schiemer and Prosser 1976; Nuttall 1985; Nuttall et al. 1985). Organic and inorganic silt particles that stick to filamentous or meshlike algae may contribute substantially to the weight of the epiphyton complex. Menzie (1979) found as much as 3.8 g of particulate material attached per gram of *M. spicatum*.

107. The effect of increased water temperature resulting from thermal effluent on the growth of epiphytic algae was described by Hickman and Klarer (1974). An extended growing season was responsible for early epiphyton development, but temperature alone was not the reason for all the difference. Day length and light intensity were also responsible.

108. Hodgson and Carter (1982) estimated the effect of *Hydrilla* herbicide treatment on a periphyton community. They used glass slide periphyton samplers instead of assessing periphyton directly on *Hydrilla* plants. Nevertheless, the growth of periphyton was higher following the treatment compared with the untreated control. Anderson (1981) described the changes in species diversity of periphyton in a small macrophyte pond following a treatment by

hexazinone. The species diversity of periphyton was dramatically decreased after the treatment.

Phytoplankton

109. Numerous papers refer to the relationship between macrophytes and surrounding phytoplankton with often contradictory conclusions. Hasler and Jones (1949) were among the first limnologists to study this relationship in outdoor experiments. According to their results, a dense stand of submersed macrophyte *E. canadensis* significantly inhibited the growth of phytoplankton. Hogestu et al. (1960) also described an antagonistic relationship between rooted aquatic macrophytes (*Hydrilla, Vallisneria, Nymphoides*) and phytoplankton. The inhibition of phytoplankton growth was explained by shading effect and competition for nutrients plus some other unknown factors. Fitzgerald (1969) concluded that even if the main reason for the antagonistic relationship is based upon nutritional factors (nitrogen-limited cultures of macrophytes will remain relatively free of algae), there are indications of antibiotic factors as well. Planas et al. (1981) have shown that phenolic compounds extracted from *M. spicatum* can inhibit the growth of algae in unialgal cultures and in natural assemblages in the laboratory.

110. Besides papers describing the limiting effects of macrophytes on phytoplanktaon, others report the inhibition of macrophyte growth by the abundance of phytoplankton. Jones et al. (1983) suggested that a major increase in phytoplankton abundance that resulted in a marked decrease of light penetration might be, at least partly, responsible for the decline of *M. spicatum* in Lake Wingra, WI. The growth of the submersed macrophyte *Zannichelia peltata* can be significantly inhibited by an algal filtrate (Van Vierssen and Prins 1985). Algal culture consisted mainly of *Anabaena*, and it was concluded that this alga released an unspecified allelopathic substance. Sharma (1985) found that the growth of *Eichhornia crassipes* was inhibited when grown in water containing algae such as *Scendesmus bijugatis* and *Chlorella pyranoidosa*. Waterhyacinth plants ultimately died after 90 to 100 days of growth with these algae. The death of the plants was suspected to be due to allelopathic interactions between algae and waterhyacinths. The fungus *Alternaria eichhorniae* was isolated from the dying plants. The waterhyacinth may have become

susceptible to the fungus because it was weakened by the allelopathic effect of algae.

111. Results of experiments on the interaction between *M. spicatum* and phytoplankton indicate that *M. spicatum*, especially at the early stages of its growth, stimulated the growth of the phytoplankton (Godmaire and Planas 1983). One possibility is that extracellular organic matter released by *Myriophyllum* could be used directly or could influence indirectly the growth of phytoplankton. In their recent study, Godmaire and Planas (1986) confirmed their previous results. Multivariate analysis results showed that differences in phytoplankton productivity among sites with and without *Myriophyllum* were unrelated to nutrients and light. A factor not measured in their study must have been responsible for stimulation of phytoplankton growth. Landers (1982) studied the effect of naturally senescing aquatic macrophytes (e.g., *M. spicatum*) on nutrient chemistry and chlorophyll *a* of surrounding waters. He observed a substantial increase of phytoplankton because of organic substances released by senescing *Myriophyllum*.

Fungi

112. Among the main groups of fungi (*Myxomycetes, Ascomycetes, Basidiomycetes*, and Fungi imperfecti), there are some aquatic species. As zoospore producing organisms, fungi are well adapted to infect submersed aquatic plants. Until the early seventies, there were only occasional reports on fungal infection of aquatic plants, but no extensive, systematic research had been done. The increasing interest in biological control of nuisance aquatic weeds stimulated a research program on biological control of aquatic weeds at the Commonwealth Institute of Biological Control in Bangalore, India (Zettler and Freeman 1972). In 1970 a project on the evaluation and subsequent use of plant pathogens as biocontrol agents for aquatic weeds was begun at the University of Florida, Gainesville (Freeman 1977). Both endemic and exotic plant pathogens (mostly fungi) were collected and tested (Freeman et al. 1974, 1981, 1982; Freeman 1979). The Aquatic Plant Control Research Program (APCRP) has been coordinated by the US Army Engineer Waterways Experiment Station (WES), Vicksburg, MS.

113. Table 2 presents a list of potentially pathogenic fungi that were reported from aquatic plants. In Table 3 the same fungi are arranged

according to their macrophyte hosts. Besides freshwater species, *Spartina* and seagrasses from brackish waters (*Zostera, Ruppia*) were included. Only several selected examples of fungal microflora on *Spartina* are presented. Gessner and Kohlmayer (1976) list about 100 fungus species that have been reported from *Spartina*. As this plant is not a central point of interest, these fungi are not included in the table. Table 3 lists 150 species of fungi from 47 different aquatic plant species. There seems to be considerable host specificity (with the exception of *Rhizoctonia solani*) reported from 16 different plant species. Quite common were genera *Cercospora* (nine species), *Fusarium* (seven species), and *Pythium* (seven species); all of them are known as cosmopolitan parasites. A common aquatic smut *Doassania*, known to be widespread on aquatic plants, was also reported from several plant species.

114. From the biological control point of view, most research has been done on waterhyacinth. Several fungus species were found to exhibit at least weak pathogenicity to waterhyacinth (see Table 3). Many of them were tested in laboratory or field tests (Charudattan 1973, 1981; Conway and Freeman 1977, Jamil et al. 1983; Lin and Charudattan 1975; Ponnappa 1973; Rahim and Tawfig 1984; Rintz 1973). Often their capacity for infecting a wide range of plants was screened as well. The most promising species were tested in small- and large-scale field tests mostly in the States of Florida and Louisiana.

115. *Cercospora rodmanii* has shown good potential as a biological control agent (Freeman et al. 1982). It is an endemic fungus that invades waterhyacinth readily by the way of stomata on leaves and petioles. It causes leaf-spotting with resultant death of severely infected leaves. An epiphytotic can be induced by spraying waterhyacinth with either freshly prepared or formulated inoculum. Once established, the fungus spreads by airborne conidia to plants in adjacent areas. A formulation of *C. rodmanii* has been produced commercially by Abbott Laboratories. Agents for potential use in enhancing the germination of spores in the formulation were tested by Pennington and Theriot (1982). *Cercospora piaropi*, which is closely related to *C. rodmanii* in both morphology and disease symptomology, was reported as a cause of severe, large-scale damage on waterhyacinth in Lake Conroe, TX (Martyn 1985).

116. In recent years, several research projects have concentrated on biological control of *Hydrilla* and *Myriophyllum*. An isolate of *Fusarium roseum* "Culmorum" isolated from *Stratiotes aloides* near Wageningen, Holland,

was found to be pathogenic to *H. verticillata* (Charudattan et al. 1980, 1984). As the results were very promising, it was decided to test the fungus on *Hydrilla* in a large-scale study. Although the treated plants were more damaged than the controls, a practical level of biocontrol was not achieved. Pennington (1984, 1985) screened numerous isolates of bacterial and fungal epiphytes from *Hydrilla* for production of enzymes that can lyse specific plant components. Several cellulase-producing fungi were capable of damaging *Hydrilla* significantly in test tube assays. The results of aquaria experiments did not confirm the preliminary tests, apparently because the inoculum used for aquarium tests did not have all the necessary additional nutrients or metabolites that were present in the inoculum used for test tube tests. The results also indicated that *Hydrilla* plants might display a different degree of resistance to cellulolytic fungi depending on their previous life history. A similar approach was used by Gunner (1983, 1984), who inoculated *M. spicatum* and *M. heterophyllum* with enzyme-enhanced pectinolytic or cellulolytic microorganisms originally isolated from these species, which significantly accelerated plant necrosis. Among several isolates Gunner tested, a very promising one was the fungus *Mycoleptodiscus terrestris*. Andrews and Hecht (1981) and Andrews et al. (1982) studied the relationship between *M. spicatum* and the fungus *Acremonium curvulum*. *Acremonium* is apparently pathogenic to milfoil when milfoil is grown under conditions of stress.

117. A survey for pathogens of aquatic weeds was done in northern California during 1980 and 1981. Several fungal isolates proved to be pathogenic to their respective hosts (Bernhardt and Duniway 1985, 1986). The most promising for the potential use in biological control was *Pythium carolinianum* pathogenic to *Myriophyllum aquaticum* (syn. *brasiliense*) (Bernhardt and Duniway 1984).

118. Among numerous papers on fungi associated with seaweeds, at least one should be mentioned here. Miller and Jones (1983) described the dependence of traustochytrids on the amount of carbohydrates released by senescing *Fucus* thalli. Traustochytrid numbers were much lower on young and mature host plants than on the senescing ones.

119. Much research has been done on the role of fungi as decomposers of dead organic matter. Over 100 species of higher filamentous fungi have been reported from saltmarsh grasses from the genus *Spartina* (Gessner and Kohlmayer 1976). Twenty isolates of these fungi were surveyed for their ability to

produce degradative enzymes (Gessner 1980). Enzymes capable of degrading cellulose, cellobiose, lipids, pectin, starch, tannic acid, and xylan were detected. One of the fungi occurring most frequently on *Spartina*, *Buergenerula spartinae*, was tested for its polysaccharidase activities. Nine polysaccharidase-type enzymes were detected with xylanase and cellulase being the most active ones (Torzilli and Andrykovitch 1980). No pectic enzyme activity was detected.

120. Besides enzymes, fungi are known to produce antibiotics and toxins. Stevens et al. (1979) analyzed a filtrate of the culture of *A. eichhorniae* growing in potato-dextrose broth. The filtrate was able to induce disease symptoms in waterhyacinth. The main compound of the filtrate was isolated and described as bostrycin, which is an antibiotic against gram-positive bacteria. Bostrycin itself did not show any effect on waterhyacinth, which means that some other constituent in the filtrate, even if in a very low concentration, was biologically active against the plant. Charudattan and Rao (1982) tried to isolate the toxic substance from *A. eichhorniae*. They also isolated 4-deoxybostrycin and isopropylidene derivatives. All four purified products exhibited phytotoxicity against waterhyacinth and may have potential as broad-spectrum herbicides.

121. Rejmankova et al. (1986) found a filtrate from culture of *Pythium myriotylum* to be very effective in killing duckweeds (*L. gibba*). There is a strong possibility that a phytotoxin may be involved in pathogenicity. Phytotoxins have been isolated from several species of *Pythium* (Martin 1964), including *P. myriotylum* (Csinos and Hendrix 1978). Besides being able to produce toxins, several *Pythium* species are also known to be cellulolytic (Deacon 1979). Different *Pythium* species have often been reported as pathogenic not only to freshwater vascular plants but also to filamentous algae (Beck and Erb 1984) and seaweeds (Kazama and Fuller 1970, Aleem 1980).

Viruses

122. Although the term "virus" has been used from about 1890, knowledge of plant viruses has increased markedly in the last few decades mainly as a result of intensified research by both molecular biologists and plant pathologists. Viruses can be defined, according to Stevens (1983), as submicroscopic particles made of one or more pieces of a single species of nucleic acid, RNA

or DNA, surrounded by proteins. These particles replicate alone or in the presence of similar structures, but only in living cells, using at least some of the host cell enzymes. The dimensions of viruses are usually determined by electron microscopy and measured in nanometers (10^{-9} m). Viruses enter and multiply in a wide range of hosts. They have been recorded from numerous plant families, but those from plants of economic importance have been studied most and are best documented. Each virus is named according to the major host with which it is associated and also the symptoms produced in that host. However, a plant virus may invade a number of different plant species, producing different symptoms in each. Nomenclature and classification of plant viruses are described by Smith (1977).

123. Viruses produce visible or otherwise detectable abnormalities in plants. The most obvious symptoms are external and take the form of foliage color changes: mosaicking, mottling, yellowing, ringspot, and local lesions (Stevens 1983). There are many alterations in metabolism in virus-infected plants, e.g., changes in the pattern of carbohydrate accumulation that may be caused by a limited availability of orthophosphate in virus-infected tissues brought about by an accelerated demand for viral nucleic acid synthesis. Orthophosphate deficiency causes a reduction in the movement of triose phosphate from the chloroplast to the cytoplasm and an inhibition of transport of photoassimilates (Misaghi 1982).

124. The spread or transmission of viruses from one plant to another can be mechanical, or an organism called a "vector" can be involved. The following organisms are often recognized as vectors for viruses: insects (namely aphids), mites, nematodes, and fungi.

125. Only a few papers describe viruses in aquatic plants. MacClement and Richards (1956) in their contribution on viruses in wild plants repeatedly observed virus-type infection in *L. minor*, *P. pectinatus*, *P. crispus*, *Ceratophyllum*, and *Nymphaea*. The peak of virus infection was closely connected with the maximum growth of individual species. The frequency of disease found in species sampled in a random survey was about 7 percent for the aquatic species. Pettet and Pettet (1970) reported a massive dieback of *Pistia stratiotes* in the Ibadan area of Western State, Nigeria, associated with a virus infection. The infection seemed to be spread by the aphid *Rhopalosiphum nymphaeae*. The authors apparently did not try to isolate the virus. There were attempts to explain *M. spicatum* decline in the Chesapeake Bay as a result of

virus infection (Bayley et al. 1968). In a later paper, Bayley (1970) stated that she had not been able to isolate any virus from *Myriophyllum* from that area. Stunted plants of alligatorweed (*A. phyloxeroides*) were found in Florida. Flexous-rod particles 1.717 mm in diameter were seen in negatively stained leaf extracts. They were similar to the beet yellow group of viruses. Attempts to transfer a pathogen to healthy plants by manual inoculation or by *Apis gossypii* were unsuccessful (Hill and Zettler 1973). Jones (1980) investigated the cause of leaf mottling of *Spartina* and was able to purify and describe a new virus that is distantly serologically related to agropyron mosaic virus. The name "spartina mottle virus" was proposed for this newly recognized virus. There is a short note in the Proceedings of the Conference on Strategies for Aquatic Weed Management (Chestnut 1982) about viruses, or viruslike particles, found in *Hydrilla* and *Ludwigia*, but no more information is given.

126. Several papers describe algal viruses. A virus pathogenic to certain blue-green algae belonging to the genera *Plectonema, Phormidium*, and *Lyngbya* has been isolated from a variety of freshwater habitats in Scotland and has been named D-1 (Daft et al. 1970). This virus has similar characteristics to the LPP-1 virus isolated and described in the United States by Safferman and Morris (1964). The virus causes lysis of the host cell and rapid loss of phycobilin and chlorophyll pigments. Review and summary of the state of art in algal virology until 1972 were presented by Brown (1972), who described the virus *Chara corallina* (CCV), which was isolated, characterized, and used to experimentally infect virus-free *Chara* cells (Skotnicki et al. 1976). Van Etten et al. (1985) and Schuster et al. (1986) described several plaque-forming viruses of the green unicellular *Chlorella*-like algae. They were grouped into 11 classes of PBCV-1 viruses. A list of eucaryotic algae in which viruslike particles have been observed by electron microscopy was published by Dodds (1979). Several investigations carried out under field conditions tested the possible utilization of viruses as control of unwanted algae (Jackson and Sladecek 1970). Algal viruses might serve as "ideal" algicides, but much research still remains to be done.

127. More research must be done before the use of viruses as a potential control tactic for higher aquatic plants can be considered. There is certainly an enormous gap between information on viruses of crop plants where a

lot of genetic engineering has been employed recently (Shewmaker et al. 1985) and that on viruses infecting aquatic plants, which is almost nonexistent.

Nematodes

128. Nematodes are bilaterally symmetric, cylindroid, unsegmented, bisexual, triploblastic organisms comprising a separate phyllum *Nematodae*. Nematodes occurring practically everywhere that life can be supported, inhabit a wide variety of environments, and they are the most numerous of all metazoa. They are found in all soils from the polar region to the tropics, whether arid or humid; they are abundant in the bottom sediments of lakes, rivers, and the oceans. The biosphere is carpeted with a layer of nematodes several centimetres thick (Nicholas 1984). All nematodes, however, even those in soil, are more or less aquatic since they require in the active stage a moisture film in which to move and through which to breathe.

129. Worldwide recognition of nematodes as important causal agents of plant diseases did not occur until the middle of this century. The most obvious adaptation to parasitism in phytoparasitic nematodes is their universal possession of a buccal stylet (Zuckerman et al. 1971). The stylet looks like a miniature hypodermic needle. A nematode feeds on the plant by puncturing the cell wall with this stylet. Through the stylet, enzymes are released into the plant cells. Then, as the high-molecular nutrient substances (proteins, carbohydrates, etc.) are degraded to simpler compounds by the action of these enzymes, the nematodes begin to suck up the food through the stylet. An external, extraintestinal digestion takes place. Species of some genera (e.g., *Meloidogyne* and *Heterodera*) were found to produce feeding tubes (Rumpenhorst 1984). These seem to be common and lasting structures produced at the feeding sites of sedentary root nematodes. Sedentary root nematodes induce the formation of syncytia and giant cell complexes. The feeding tubes, formed by hardening saliva, are connected to the stylet orifice. The feeding tube is assumed to be a duct into which the plant cell secretes special products and through which these secretions are directed into the feeding ampulla. The nematode feeds on the content of this ampulla. The nematode takes in these secreted products rather than common components of cytoplasm.

130. On the basis of their feeding habits, parasitic nematodes are divided into two main groups:

a. Endoparasites. These enter the plant and feed from inside. Some nematodes move within the tissues and force their way between cells, injuring the tissues as they feed.

b. Ectoparasites. These do not enter the plant. They feed from outside and rarely penetrate the host tissues.

Plants frequently suffer from more than one disease. Nematodes are notorious partners in plant disease complexes. They act as follows:

a. Wounding agents. Wounds and punctures provide entry points for other pathogens; once bacteria or fungi are inside, they survive in the tunnels made by the nematodes.

b. Host modifiers. Digestive enzymes excreted by nematodes change the nutrient contents of the host plant so that it is more palatable not only for nematodes but also for other pathogens as well.

c. Vectors. The nematode stylet is very small but still big enough for carrying viruses; also, spores can stick to nematode bodies and be transported.

131. The influence of nematodes on fusarium wilts is a well documented and widely occurring example of synergistic interactions between nematodes and fungi enhancing pathogenicity. Mousa and Hague (1985), for example, described an experiment in which fusarium wilt resistant and susceptible cultivars of soybean were exposed to both *Fusarium oxysporum* and *Meloidogyne incognita* (nematode). Both resistant and susceptible cultivars were severely wilted when nematodes were introduced at the same time or about 2 weeks earlier than *Fusarium*. The interaction of the nematode *Criconemella xenoplex* and *Fusarium* on the growth of peaches was studied by Nyczepir and Pusey (1985). When seedlings were treated with *Fusarium* and nematodes, severe symptoms of necrosis were found in the treatment in which nematode inoculation preceded *Fusarium* about 4 weeks. Similar results were obtained by Pelz et al. (1983), who found that the wilt pathogen of the tomato, *F. oxysporum*, is not pathogenic to cucumber in the absence of nematodes (*M. incognita*), but if cucumber plants are simultaneously attacked by nematodes and *Fusarium*, wilt symptoms develop. Waller and Bridge (1984) showed several other examples of the same phenomenon (see Table 26.1 of their paper).

132. Waller and Bridge (1984) stressed that nematode damage does not simply allow easier entry of the fungus into the host; active predisposition of the whole vascular system is also involved (e.g., due to increased production of auxins).

133. Until recently there have not been much data published on nematodes living as commensals or parasites on aquatic plants. Hopper and Meyers (1967) studied the ecology of nematodes in a seagrass community. The microbial microcosm in *S. alterniflora* internodes was described by Gessner et al. (1972); among other microorganisms, the nematodes of the genus *Oncholaimus* were a frequent part of the microcosm. Potential regulating factors of nematodes and other meiofauna in *Spartina* salt marsh in Louisiana were studied by Fleeger et al. (1982). Seasonal changes in epiphytic nematodes in a brackish fjord in Finland were described by Jensen (1984).

134. One of the first reports on a freshwater parasitic nematode was on *Aphelenchoides fragariae* collected on several aquatic plant species in Florida (Smart and Esser 1968). Later, Esser et al. (1985) published a survey of phytoparasitic and free-living nematodes associated with aquatic macrophytes in Florida. They detected 25 genera and 38 species of phytoparasitic nematodes and 52 genera of free-living nematodes. The objective of the survey was to find one or more phytoparasitic nematodes that might serve as biological control agents for noxious macrophytes. Among several other phytoparasitic nematodes, *Hirschmanniella caudacrena* was found in very high numbers in the stems and leaves of *C. demersum*. Nematode densities were as high as 58 nematodes/g of fresh plant tissue (Gerber and Smart 1984). Major symptoms of nematode infestation are varying degrees of plant chlorosis, irregular growth in the form of twisted stems, and development of fewer shoots. Laboratory tests have verified that *H. caudacrena* is pathogenic to *Ceratophyllum* (Gerber et al. 1986a). Gerber et al. (1986a) also studied the infestation of *Hydrilla* with parasitic *A. fragariae*. High densities of the nematode were found in *Hydrilla* buds. The nematodes fed ectoparasitically on the meristem, the leaf primordia, the bud scales, and at the base of buds. The apical meristem of many buds was damaged or completely destroyed. *Aphelenchoides* species are active swimmers and are able to move in any direction in the water. This mobility promotes the spread of nematodes to new host plants and could be important concerning the possible use of this nematode for biocontrol of *H. verticillata* (Gerber et al. 1986a).

135. Nematodes occurring in the rhizosphere of aquatic macrophytes, namely *Potamogeton*, are described by Prejs (1977, 1986). She found that tissue damage appearing as differently colored necrotic patches on rhizomes of *Potamogeton* resulted from nematode (mainly *Hirschmanniella*) feeding.

136. Gerber et al. (1986b) prepared a comprehensive catalog of plant parasitic nematodes associated with aquatic and wetland plants. Table 4 shows several selected examples of aquatic plant-nematode associations. The occurrence of nematodes on several aquatic plant species was described also by Gaevskaya (1969). Aquatic plant nematodes do not seem to be very host specific. The most widespread among aquatic plants are the genera *Hirschmanniella* and *Aphelenchoides*. Table 4 includes 35 plant species and 32 nematode genera. *Hirschmanniella* occurred on 17 and *Aphelenchoides* on 11 plant species. *Meliodogyne*, *Dolichodorus*, and *Helicotylenchus* were also quite common; each of them occurred on 8 plant species.

PART IV: SENESCENCE AND PATHOGEN INTERACTION: ITS ADVANTAGES AND LIMITATIONS

137. Many data exist supporting the idea that senescent plants are more susceptible to pathogen infection than nonsenescent plants. The exact mechanism responsible for this phenomenon is not known. There is probably more than one reason, but, generally, a senescent plant is weaker and less resistant than nonsenescent ones.

138. Senescence proceeds as a natural part of plant development controlled primarily by internal genetic and correlative factors, but senescence can be induced also by unfavorable environmental factors. Table 5 summarizes the possible means of senescence induction and indicates which of them might be used to manipulate the senescence of undesirable aquatic weeds in the field.

139. The environmental factors do not always induce senescence in the whole population of a plant species. Only a few less vigorous plants may become senescent and die while the rest continue growing. The application of a pathogen at the proper moment, i.e., when the population is partially weakened, may greatly enhance its spread. The scheme in Figure 5 shows the possible interactions of induced senescence with pathogens. Nothing, so far, is known about the possibility of inducing pathogenicity in opportunistic microorganisms that would then attack plants and cause their senescence and, eventually, death.

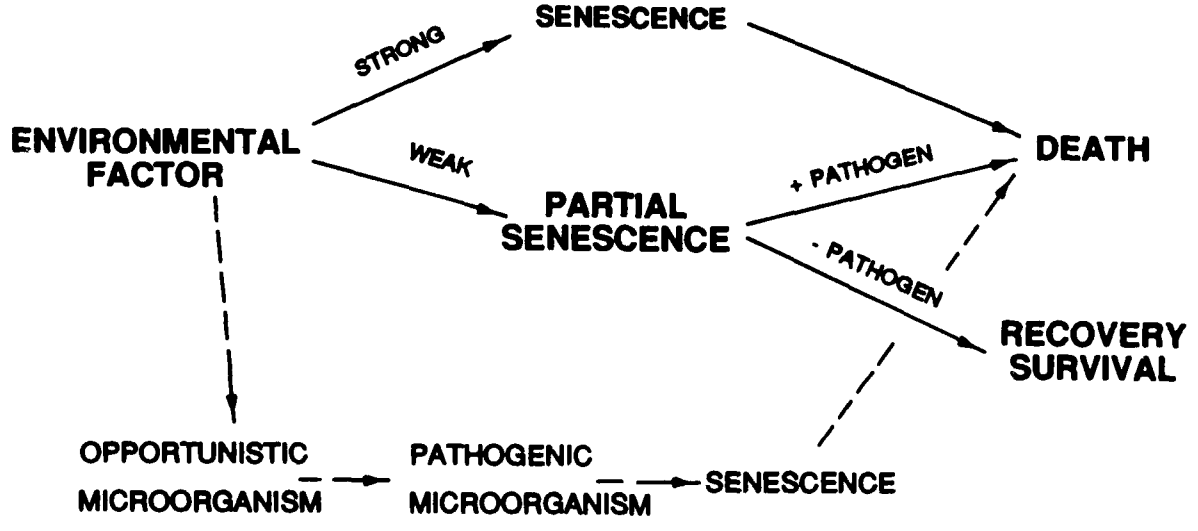

Figure 5. Scheme of interactions between environmentally induced senescence and pathogens

140. More research is needed before the combined effect of senescence and pathogens can be used in practice. It will be necessary to find what is the most practical factor for inducing senescence in a particular species, what type of pathogen is the most effective, at which stage of senescence a pathogen should be applied, etc. Limitations include varying responses of a plant species to the factor inducing senescence, unpredictable interactions of a pathogen with another microorganism present in water, and development of resistance of plants to pathogens.

PART V: CONCLUSIONS AND RECOMMENDATIONS

Conclusions

Senescence

141. The main facts regarding senescence are as follows:

a. Senescence is an important and not very well-understood stage in the plant life cycle. It is controlled by internal and external (environmental) factors. The precise mechanism of senescence induction is not known, but, in general, the initiation of senescence involves an imbalance in the relative levels of growth hormones; this change in hormone status can be caused by internal factors or environmental stimuli.

b. Among the environmental stimuli involved in senescence initiation, the following were reported: light, day length, temperature, mineral nutrients, and pathogens. When pathogens attack plants, it is not always known whether hormonal imbalances are the cause or the result of infection.

c. Senescence is accompanied by a change in enzyme activities. Peroxidases, glutamate dehydrogenase, endopeptidases, and some hydrolases have been reported to increase their activities during senescence. Dehydrogenases, ribulosebiphosphate carboxylase, glutamine synthetase, and glutamate synthase generally decrease their activities during senescence.

d. An extensive literature search identifies cytokinins as the most generally effective senescence-retarding growth regulators. Abscisic acid (ABA) and ethylene, on the other hand, are known as promoters of senescence. In many cases, cytokinins and ABA interact in a competitive manner.

e. Decreases in chlorophyll content and protein amount are most often measured as senescence characteristics. Senescence may start long before changes in these parameters become apparent. No universal marker of senescence has been found to date.

Microorganisms on aquatic plants

142. The review on microorganisms on aquatic plants is concluded as follows:

a. Aquatic macrophytes often serve as a substratum for epiphytic microorganisms, namely algae, bacteria, and fungi. The amount and diversity of epiphytic microorganisms generally increase with the age of their host mainly due to the increase in organic matter excreted by the aging host plant.

b. Microorganisms live mostly as commensals (saprophytes) on their hosts but may become parasitic as the hosts undergo stress conditions or are approaching senescence.

c. In submersed aquatic plants that usually have a very thin and reduced cuticle, bacteria do not need wounds for entry into plants. Bacteria often invade and degrade epidermal cell walls. Some are known to produce lytic enzymes. Some bacteria were reported as being able to produce antibiotics.

d. Fungi are usually regarded as the main decomposers of dead organic matter in aquatic ecosystems. Many species are known to produce enzymes capable of degrading cellulose, pectin, and starch. Besides enzymes, some fungi also produce toxins and antibiotics. The phytotoxicity of fungi has a potential use as bioherbicides. In this study, 150 fungal species were found to be reported as potential parasites on aquatic plants.

e. Epiphytic algae do not usually cause any harm to their host plants unless the colonization is so dense that it shades plants or, especially in combination with inorganic silt particles, it becomes so heavy that the host plants are damaged and dragged to the bottom.

f. Few viruses were reported from aquatic plants. A potential for biological control may be here, but at this point data are insufficient to even consider this possibility.

g. Nematodes are known to contribute to macrophyte degradation in certain cases. They wound the tissue, thus making easy infection entry. So far, at least 32 genera of nematodes parasitic on aquatic plants have been reported.

143. Two main points can be made from this literature search:

a. Senescence is a process that can be induced by changing the environmental conditions.

b. Plants in the senescent stage are more susceptible to pathogens than young or mature but nonsenescent plants.

Recommendations

144. The following research is recommended:

a. Find the most efficient means of inducing senescence in aquatic weeds that can be eventually applied on a large scale. This would include laboratory tests following the effect of algal epiphytic microflora, light, temperature, nitrogen deficiency, growth regulators (ABA), and sublethal herbicide applications on senescence in selected aquatic plants. These tests should be preceded by another set of experiments aimed at the selection of the most convenient senescence characteristics. Characteristics like chlorophyll and anthocyanin content, protein content, mineral composition of plant biomass, endogenous ABA concentrations, and activities of selected enzymes should be compared in senescing and nonsenescing plants. Within a given aquatic macrophyte species, senescence "markers" should be identified.

b. Evaluate the effectiveness of a combination of induced senescence with pathogen application. This requires tests on application of pathogens (fungal or bacterial) to aquatic weeds in different stages of senescence, both natural and induced. Attention should be paid to vegetative propagules (turion, tubers) formation in plants with induced senescence. Their susceptibility to pathogens may differ from that of senescent vegetative shoots.

c. Study the effect of a combination of induced senescence with naturally occurring microorganisms (opportunistic pathogens).

d. If small-scale research proves that the manipulation of senescence in aquatic weeds following pathogen application is feasible, field tests on a large scale should follow.

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Table 1

List of Epiphytic Bacteria Associated with Aquatic Plants

Plant Species	Type of Bacteria	Reference
Equisetum sp.	*Azotobacter*	Kudryavstev (1984)
Hydrilla verticillata	"Gram negative, nonmotile rods"	Waite and Kurucz (1977)
	Pseudomonas	Pennington (1985)
	Acinetobacter	
	Aeromonas	
	Flavobacterium	
	Bacillus	
	Enterobacter	
	Alcaligena	
	Flexibacter	
	Erwinia	
	Myconostoc	
	Rhodopseudomonas	
	Serratia	
	Caulobacter	
	Agrobacterium	
	Hafnia	
	Klebsiella	
	Sporocytophaga	
Lemna paucicostata	"Rod-shaped, cocoid bacteria"	Patience et al. (1983)
Myriophyllum heterophyllum	"Gram negative rods, pseudomonad type"	Gunner (1983)
Myriophyllum spicatum	*Heterophyllum* sp.	Gunner (1983)
	Pectinolytic isolate Br-2	Gunner (1983)
	Cyanocterial consortium	Gunner (1983)
Najas flexillis	*Caulobacter* sp.	Allen (1971)
	Pseudomonas sp.	Allen (1971)
Potamogeton pectinatus	*Bacillus* sp.	Howard-Williams and Davies (1978)
	Caulobacterium sp.	Robb et al. (1979)
	"Rough and smooth walled bacilli short rods, gram positive"	Robb et al. (1979)
Potamogeton sp.	*Azotobacter*	Kudryavstev (1984)
Sagittaria sp.	*Azotobacter*	Kudryavstev (1984)

(Continued)

Table 1 (Concluded)

Plant Species	Type of Bacteria	Reference
Spartina alterniflora	*Metallogenium*	Gessner et al. (1972)
	Hyphomicrobium	Gessner et al. (1972)
	Mycoplasma	Gessner et al. (1972)
Typha angustifolia	*Cytophaga* group	Mason and Bryant (1975)
	Pseudomonas fluorescens	Mason and Bryant (1975)
	Pseudomonas marginalis	Mason and Bryant (1975)
	Erwinia sp.	Mason and Bryant (1975)
Zostera marina	"Long rods"	Newel (1981)
"Intertidal seaweeds"	*Pseudomonas-Alteromonas* group	Lemos et al. (1985)

Table 2

Fungi Reported as Potential Pathogens from Aquatic Plants

Fungus	Host Plant	Reference
Plasmodiophorales (Plasmodiophoromycetes)		
Ligneria junci	*Alisma plantago-aquatica*	Index of Plant Diseases
Tetramyxa parasitica	*Ruppia cirrhosa*	Verhoeven (1975)
Labyrinthulaes (Labyrinthulomycetes)		
Labyrinthula sp.	*Zostera marina*	Renn (1936)
Chytridiales (Chytridiomycetes)		
Cladochytrium maculare	*Alisma plantago-aquatica*	Index of Plant Diseases
Reesia amoeboides	*Lemna minor*	Wagner (1969)
Blastocladiales (Chytridiomycetes)		
Physoderma sp.	*Myriophyllum spicatum*	Sparrow (1974)
Physoderma thilumalacharii	*Scirpus articulatus*	Pavgi and Singh (1980)
Lagenidiales (Oomycetes)		
Lagenidium muenschari	*Potamogeton* sp.	Index of Plant Diseases
Saprolegniales (Oomycetes)		
Saprolegnia asterophora	*Spirogyra* sp.	Beck and Erb (1984)
Peronosporales (Oomycetes)		
Albugo bliti	*Alternanthera phyloxeroides*	Index of Plant Diseases

(Continued)

Table 2 (Continued)

Fungus	Host Plant	Reference
Peronosporales (Oomycetes) (Continued)		
Pythium afertile	*Elodea canadensis*	Bernhardt (1983)
Pythium afertile	*Myriophyllum spicatum*	↓
Pythium afertile	*Potamogeton crispus*	↓
Pythium afertile	*Potamogeton pectinatus*	↓
Pythium carolinianum	*Myriophyllum brasiliense*	↓
Pythium carolinianum	*Myriophyllum spicatum*	↓
Pythium debaryanum	*Phragmites communis*	Index of Plant Diseases
Pythium ultimum	*Phragmites communis*	Index of Plant Diseases
Pythium gracile	*Spirogyra* sp.	Beck and Erb (1984)
Pythium helicoides	*Typha latifolia*	Index of Plant Diseases
Pythium myriotylum	*Lemna gibba*	Rejmankova et al. (1986)
Pythium myriotylum	*Lemna minor*	Rejmankova et al. (1986)
Pythium myriotylum	*Spirodela Polyrrhiza*	Rejmankova et al. (1986)
Pythium sp.	*Eichhornia crassipes*	Charudattan (1973)
Pythium sp.	*Hydrilla verticillata*	Varghese and Singh (1973)
Pythium sp.	*Nuphar luteum*	Van der Velde (1978)
Pythium sp.	*Nymphaea odorata*	Index of Plant Diseases
Pythium sp.	*Nymphaea tuberosa*	Index of Plant Diseases
Pythium sp.	*Potamogeton nodosus*	Bernhardt (1983)
Pythium sp.	*Potamogeton pectinatus*	Lumsden et al. (1963)
Pythium sp.	*Potamogeton perfoliatus*	Motta (1978)
Pythium sp.	*Ruppia maritima*	Motta (1978)
Pytopthora parasitica	*Hydrilla verticillata*	Freeman (1977)
Pythiogeton autossytum	*Typha latifolia*	Index of Plant Diseases
Helotiales (Ascomycotina)		
Pezizella oenontherae	*Lythrum salicaria*	Index of Plant Diseases

(Continued)

Table 2 (Continued)

Fungus	Host Plant	Reference
Hypocreales (Ascomycotina)		
Claviceps nigricans	*Eleocharis acicularis*	Conners (1967)
Claviceps purpurea	*Phragmites communis*	Index of Plant Diseases
Rhytismatales (Ascomycotina)		
Lophodermium typhinum	*Typha latifolia*	Index of Plant Diseases
Sphaeriales (Ascomycotina)		
Buergenerula spartinae	*Spartina alterniflora*	Torzilli and Andrykovitch (1980)
Chaetomium funicolum	*Myriophyllum spicatum*	Bernhardt (1983)
Coniochaeta sp.	*Heteranthera dubia*	Bernhardt (1983)
Guignardia cepalariae	*Alternanthera phyloxeroides*	Index of Plant Diseases
Hendersonia arundinacea	*Phragmites communis*	Index of Plant Diseases
Hendersonia typhae	*Typha latifolia*	Index of Plant Diseases
Leptosphaeria culmorum	*Eleocharis pervula*	Conners (1967)
Leptosphaeria eustoma	*Typha latifolia*	Lowe (1969)
Leptosphaeria typharum	*Typha latifolia*	Index of Plant Diseases
Lulworthia sp.	*Zostera marina*	Newel (1981)
Mycosphaerella pontederiae	*Nuphar advena*	Index of Plant Diseases
Mycosphaerella pontederiae	*Nymphaea odorata*	Index of Plant Diseases
Mycosphaerella typhae	*Typha latifolia*	Index of Plant Diseases
Mycosphaerella sp.	*Phragmites communis*	Index of Plant Diseases
Ophiobolus halimus	*Zostera marina*	Newel (1981)
Ophiobolus sp.	*Typha latifolia*	Horst (1979)
Pleospora graminis	*Phragmites communis*	Index of Plant Diseases
Pleospora typhae	*Typha latifolia*	Index of Plant Diseases
Sphaerulina pedicellata	*Spartina alterniflora*	Gessner et al. (1972)

(Continued)

Table 2 (Continued)

Fungus	Host Plant	Reference
Uredinales (Urediniomycetes)		
Nyssopsora echinata	*Oenanthe sarmentosa*	Conners (1967)
Puccinia eleocharidis	*Eleocharis palustris*	Conners (1967)
Puccinia mognusiana	*Phragmites communis*	Index of Plant Diseases
Puccinia phragmitis	*Phragmites communis*	Index of Plant Diseases
Puccinia scirpi	*Numphoides peltata*	Munda and Garrasi (1978)
Uredo eichhorniae	*Eichhornia crassipes*	Freeman et al. (1981)
Uredo maculans	*Alternanthera phyloxeroides*	Index of Plant Diseases
Uromyces acuminatus	*Spartina alterniflora*	Conners (1967)
Uromyces pontederiae	*Pontederia lanceolata*	Charudattan (1981)
Ustilaginales (Ustilaginomycete)		
Burrillia decipiens	*Nymphaea cordata*	Conners (1967)
Burrillia limnanthemi	*Nymphaea cordata*	Conners (1967)
Burrillia pustulata	*Sagittaria* sp.	Conners (1967)
Doassansia alismatis	*Alisma plantago-aquatica*	Index of Plant Diseases
Doassansia alismatis	*Alisma geyeri*	Index of Plant Diseases
Doassansia deformans	*Sagittaria* sp.	Conners (1967)
Doassansia furva	*Sagittaria* sp.	Conners (1967)
Doassansia hydrophila	*Potamogeton natans*	Lowe (1969)
Doassansia intermedia	*Sagittaria* sp.	Conners (1967)
Doassansia martanoffiana	*Potamogeton nodosus*	Conners (1967)
Doassansia obscura	*Sagittaria* sp.	Conners (1967)
Doassansia oculta	*Potamogeton* sp.	Index of Plant Diseases
Doassansia opaca	*Sagittaria* sp.	Conners (1967)
Doassansia sagittariae	*Sagittaria* sp.	Conners (1967)

(Continued)

Table 2 (Continued)

Fungus	Host Plant	Reference
Ustilaginales (Ustilaginomycete) (Continued)		
Entyloma nymphaeae	*Nuphar advena*	Index of Plant Diseases
Entyloma nymphaeae	*Nymphaea odorata*	Index of Plant Diseases
Entyloma nymphaeae	*Nymphaea tuberosa*	Index of Plant Diseases
Neovossia iowensis	*Phragmites communis*	Index of Plant Diseases
Tracya lemnae	*Spirodela polyrrhiza*	Conners (1967)
Melanconiales (Coelomycetes)		
Cryptomela typhae	*Typha latifolia*	Index of Plant Diseases
Gleosporium nymphaearum	*Numphaea tuberosa*	Conners (1967)
Marssonia sp.	*Sagittaria* sp.	Conners (1967)
Sphaeropsidales (Coelomycetes)		
Apicarpella sp.	*Eichhornia crassipes*	Freeman et al. (1974)
Chaetophoma sp.	*Hydrilla verticillata*	Charudattan (1973)
Coniothyrium sp.	*Ceratophyllum* sp.	Bernhardt (1983)
Coniothyrium sp.	*Potamogeton crispus*	Bernhardt (1983)
Hymenopsis hydrophila	*Typha latifolia*	Index of Plant Diseases
Phoma sorghina	*Eichhornia crassipes*	Rahim and Tawfig (1984)
Phoma sp.	*Myriophyllum spicatum*	Bernhardt (1983)
Phoma sp.	*Potamogeton pectinatus*	Lumsden et al. (1963)
Phyllosticta fatisscens	*Nuphar advena*	Index of Plant Diseases
Phyllosticta fatisscens	*Nuphar odorata*	
Phyllosticta nymphaeacea	*Nuphar advena*	
Phyllosticta typhina	*Typha latifolia*	
Selenophoma graminis	*Phragmites communis*	
Septoria lythrina	*Lythrum salicaria*	
Septoria oenanthis	*Oenanthe sarmentosa*	Conners (1967)
Septoria punctoides	*Eleocharis pauciflora*	Conners (1967)
Septoria villarsiae	*Nymphoides peltate*	Munda and Garrasi (1978)

(Continued)

Table 2 (Continued)

Fungus	Host Plant	Reference
Sphaeropsidales (Coelomycetes) (Continued)		
Stagnospora typhiodearum	*Typha latifolia*	Index of Plant Diseases
Stagnospora sp.	*Phragmites communis*	Index of Plant Diseases
Agnomycetales = Mycelia sterilia (Hyphomycetes)		
Papulaspora aspera	*Potamogeton crispus*	Bernhardt and Duniway (1985)
Papulaspora aspera	*Potamogeton nodosus*	Bernhardt and Duniway (1985)
Papulaspora sp.	*Potamogeton perfoliatus*	Motta (1978)
Papulaspora sp.	*Ruppia maritima*	Motta (1978)
Rhizoctonia solani	*Alternanthera philoxeroides*	Freeman et al. (1974)
	Azolla pinnata	Sasi et al. (1979)
	Hydrilla verticillata	Joyner and Freeman (1973)
	Hydrocotyle umbellata	Joyner and Freeman (1973)
	Lemna minor	Joyner and Freeman (1973)
	Limnobium spongia	Joyner and Freeman (1973)
	Myriophyllum aquaticum	Joyner and Freeman (1973)
	Myriophyllum spicatum	Freeman et al. (1981)
	Najas flexilis	Bourn and Jenkins (1928)
	Pistia stratiotes	Joyner and Freeman (1973)
	Pontederia lanceolata	Joyner and Freeman (1973)
	Potamogeton pectinatus	Bourn and Jenkins (1928)
	Potamogeton perfoliatus	Bourn and Jenkins (1928)
	Ruppia maritima	Bourn and Jenkins (1928)
	Salvinia rotundifolia	Joyner and Freeman (1973)
	Vallisneria spiralis	Bourn and Jenkins (1928)

(Continued)

Table 2 (Continued)

Fungus	Host Plant	Reference
Agnomycetales = Mycelia sterilia (Hyphomycetes) (Continued)		
Rhizoctonia sp.	*Eichhornia crassipes*	Freeman (1977)
Sclerotium hydrophyllum	*Myriophyllum spicatum*	Hayslip and Zettler (1973)
Sclerotium rolfsii	*Hydrilla verticillata*	Freeman 1977
Sclerotium sp.	*Nuphar luteum*	Johnson et al. (1976)
Sclerotium sp.	*Nymphaea odorata*	Johnson et al. (1976)
Hyphomycetales = Moniliales (Hyphomycetes)		
Acremonium curbulum	*Myriophyllum spicatum*	Andrews et al. (1982)
Acremonium zonatum	*Eichhornia crassipes*	Freeman (1977)
Acremonium sp.	*Zostera marina*	Newel (1981)
Alternaria alternantherae	*Alternanthera phyloxeroides*	Holcomb (1982)
Alternaria eichhorniae	*Eichhornia crassipes*	Sharma (1985)
Alternaria tenuissima	*Elodea canadensis*	Bernhardt (1983)
Alternaria tenuissima	*Myriophyllum spicatum*	Bernhardt (1983)
Alternaria sp.	*Nymphaea odorata*	Horst (1979)
Alternaria sp.	*Salvinia auriculata*	Loveless (1969)
Anquillospora crassa	*Potamogeton pectinatus*	Bernhardt (1983)
Aspergillus awomori	*Hydrilla verticillata*	Pennington (1985)
Aspergillus sp.	*Eichhornia crassipes*	Charudattan (1973)
Aspergillus sp.	*Hydrilla verticillata*	Freeman (1977)
Bipolaris stenospila	*Eichhornia crassipes*	Freeman (1977)
Cephalosporium sp.	*Eichhornia crassipes*	Rahim and Tawfig (1984)
Cephalosporium sp.	*Hydrilla verticillata*	Charudattan (1973)
Cephalosporium sp.	*Myriophyllum spicatum*	Bernhardt (1983)
Cephalosporium sp.	*Potamogeton perfoliatus*	Motta (1978)
Cephalosporium sp.	*Potamogeton pectinatus*	Bernhardt (1983)
Cephalosporium sp.	*Ruppia maritima*	Motta (1978)
Cercospora alternantherae	*Alternanthera phyloxeroides*	Index of Plant Diseases
Cercospora alismatis	*Alisma plantago-aquatica*	Index of Plant Diseases

(Continued)

Table 2 (Continued)

Fungus	Host Plant	Reference
Hyphomycetales = Moniliales (Hyphomycetes) (Continued)		
Cercospora alismatis	*Sagittaria* sp.	Horst (1979)
Cercospora exotica	*Numphaea odorata*	Horst (1979)
Cercospora limnobii	*Limnobium spongia*	Conway (1978)
Cercospora nymphaeacea	*Nuphar luteum*	Charudattan et al.
Cercospora nymphaeacea	*Nymphaea odorata*	Index of Plant Diseases
Cercospora piaropi	*Eichhornia crassipes*	Freeman (1977)
Cercospora pontederiae	*Pontederia cordata*	Conners (1967)
Cercospora rodmani	*Eichhornia crassipes*	Conway (1978)
Cercospora sagittariae	*Sagittaria* sp.	Conners (1967)
Cladosporium sp.	*Typha latifolia*	Index of Plant Diseases
Cladosporium sp.	*Zostera marina*	Newel (1981)
Curvularia lunata	*Eichhornia crassipes*	Rahim and Tawfig (1984)
Curvularia sp.	*Hydrilla verticillata*	Varghese and Singh (1973)
Curvularia sp.	*Potamogeton nodosus*	Bernhardt (1983)
Curvularia sp.	*Potamogeton pectinatus*	Lumsden et al. (1963)
Cylindrocarpon sp.	*Myriophyllum spicatum*	Bernhardt (1983)
Dactylella microaquatica	*Myriophyllum spicatum*	Hayslip and Zettler (1973)
Dactylella aquatica	*Potamogeton crispus*	Bernhardt (1983)
Dichotomophthoropsis numphaearum	*Brasenia schreberi*	Johnson and King (1976)
	Nuphar luteum	Johnson and King (1976)
	Nymphaea orodata	Johnson and King (1976)
	Nymphaea tuberosa	Johnson and King (1976)
Didymaria alismatis	*Alisma plantago-aquatica*	Index of Plant Diseases
Didymaria alismatis	*Alisma geyeri*	Index of Plant Diseases
Didymaria alismatis	*Sagittaria* sp.	Conners (1967)
Diplosporium sp.	*Potamogeton pectinatus*	Bernhardt (1983)
Doratomyces eichhornius	*Eichhornia crassipes*	Conway and Kimbrough (1975)
Drechslera spicifera	*Eichhornia crassipes*	Rahim and Tawfig (1984)
Eipcoccum nigrum	*Myriophyllum spicatum*	Bernhardt (1983)
Flagellospora curvula	*Myriophyllum spicatum*	Bernhardt (1983)

(Continued)

Table 2 (Continued)

Fungus	Host Plant	Reference
Hyphomycetales = Moniliales (Hyphomycetes) (Continued)		
Flagellospora curvula	*Potamogeton pectinatus*	Bernhardt (1983)
Flagellospora stricta	*Myriophyllum spicatum*	Hayslip and Zettler (1973)
Fusarium acuminatum	*Sagittaria* sp.	Conners (1967)
Fusarium equiseti	*Eichhornia crassipes*	Rahim and Tawfig (1984)
Fusarium lateritium	*Heteranthera dubia*	Bernhardt (1983)
Fusarium moniliforme	*Eichhornia crassipes*	Rahim and Tawfig (1984)
Fusarium moniliforme	*Myriophyllum spicatum*	Hayslip and Zettler (1973)
Fusarium moniliforme	*Potamogeton pectinatus*	Bernhardt (1983)
Fusarium nivale	*Myriophyllum spicatum*	Bernhardt (1983)
Fusarium oxysporium	*Myriophyllum spicatum*	Hayslip and Zettler (1973)
Fusarium roseum	*Eichhornia crassipes*	Freeman et al. (1982)
Fusarium roseum	*Hydrilla verticillata*	Charudattan et al. (1984)
Fusarium roseum	*Myriophyllum spicatum*	Hayslip and Zettler (1973)
Fusarium solani	*Eichhornia crassipes*	Jamil et al. (1983)
Fusarium solani	*Hydrilla verticillata*	Charudattan et al. (1978)
Fusarium solani	*Myriophyllum spicatum*	Hayslip and Zettler (1973)
Fusarium sporotrichoides	*Myriophyllum spicatum*	Andrews and Hecht (1981)
Fusarium tricinctum	*Myriophyllum spicatum*	Bernhardt (1983)
Geotrichium sp.	*Potamogeton crispus*	Bernhardt (1983)
Gliocephalis sp.	*Hydrilla verticillata*	Charudattan (1973)
Gliocladium roseum	*Myriophyllum spicatum*	Bernhardt (1983)
Heterosporium maculatum	*Scirpus* sp.	Lowe (1969)
Heterosporium maculatum	*Typha latifolia*	Index of Plant Diseases
Humicola sp.	*Hydrilla verticillata*	Pennington (1985)
Hyaloflorae sp.	*Potamogeton pectinatus*	Lumsden et al. (1963)
Mycoleptodiscus terrestris	*Eichhornia crassipes*	Horst (1979)

(Continued)

Table 2 (Concluded)

Fungus	Host Plant	Reference
Hyphomycetales = Moniliales (Hyphomycetes) (Continued)		
Mycoleptodiscus terrestris	*Myriophyllum spicatum*	Gunner (1983)
Myrothecium roridum	*Eichhornia crassipes*	Freeman et al. (1982)
Napicladium arundinaceum	*Phragmites communis*	Index of Plant Diseases
Nigrospora oryzae	*Potamogeton pectinatus*	Bernhardt (1983)
Nigrospora sp.	*Eichhornia crassipes*	Charudattan (1973)
Oidiodendron sp.	*Hydrilla verticillata*	Charudattan (1973)
Ovularia numphaerum	*Numphaea odorata*	Index of Plant Diseases
Paecilomyces sp.	*Ceratophyllum* sp.	Bernhardt (1983)
Papularia arundinis	*Phragmites communis*	Index of Plant Diseases
Penicillium sp.	*Hydrilla verticillata*	Freeman (1977)
Periconia sp.	*Hydrilla verticillata*	Charudattan (1973)
Pullaria pullulans	*Potamogeton pectinatus*	Lumsden et al. (1963)
Ramularia aquatilis	*Potamogeton* sp.	Index of Plant Diseases
Rhynchosporium alismatis	*Alisma plantago-aquatica*	Conners (1967)
Rhynchosporium alismatis	*Sagittaria* sp.	Conners (1967)
Scolecotrichum graminis	*Phragmites communis*	Index of Plant Diseases
Scolecotrichum typhae	*Typha latifolia*	Index of Plant Diseases
Spicariopsis sp.	*Salvinia auriculata*	Loveless (1969)
Sitgmina sp.	*Hydrilla verticillata*	Charudattan (1973)
Sigmoidea sp.	*Eichhornia crassipes*	Lin and Charudattan (1975)
Sporobolomyces roseus	*Nuphar advena*	Conners (1967)
Trichoderma viride	*Potamogeton perfoliatus*	Motta (1978)
Trichoderma viride	*Ruppia maritima*	Motta (1978)
Trichoderma sp.	*Eichhornia crasspies*	Charudattan (1973)
Trichoderma sp.	*Hydrilla verticillata*	Freeman (1977)
Trichoderma sp.	*Myriophyllum spicatum*	Bernhardt (1983)
Trichoderma sp.	*Potamogeton crispus*	Bernhardt (1983)
Verticillium sp.	*Hydrilla verticillata*	Varghese and Singh (1973)

Table 3

Aquatic Plants from Which the Pathogenic Fungi Were Reported

Plant Species	Fungus	Reference
Alisma plantago-aquatica	*Cercospora alismatis*	Index of Plant Diseases
	Cladochytrium maculare	
	Didymaria alismatis	
	Doassansia alismatis	
	Ligniera junci	
	Rhynchosporium alismatis	Conners (1967)
Alisma geyeri	*Didymaria alismatis*	Index of Plant Diseases
	Doassansia alismatis	Index of Plant Diseases
Alternanthera philoxeroides	*Albugo bliti*	Index of Plant Diseases
	Alternaria alternantherae	Holcomb and Antonopoulos (1976)
	Cercospora alternantherae	Index of Plant Diseases
	Guiguardia cepalariae	Index of Plant Diseases
	Rhizoctonia solani	Freeman et al. (1974)
	Uredo maculans	Index of Plant Diseases
Azolla pinnata	*Phizoctonia solani*	Sasi et al. (1979)
Brasenia schreberi	*Dichotomophthoropsis numphaearum*	Johnson and King (1976)
Ceratophyllum demersum	*Coniothyrium* sp.	Bernhardt (1983)
	Paecilomyces sp.	Bernhardt (1983)
Eichhornia crassipes	*Acremonium zonatum*	Freeman (1977)
	Alternaria eichhorniae	Sharma (1985)
	Apicarpella sp.	Freeman et al. (1974)
	Aspergillus sp.	Charudattan (1973)
	Bipolaris stenospila	Freeman (1977)
	Cephalosporium sp.	Rahim and Tawfig (1984)
	Cercospora piaropi	Freeman (1977)
	Cercospora rodmanii	Conway (1975)
	Curvularia lunata	Rahim and Tawfig (1984)
	Doratomyces eichhornius	Conway and Kimbrough (1975)
	Drechslera spicifera	Rahim and Tawfig (1984)
	Fusarium equiseti	Rahim and Tawfig (1984)
	Fusarium moniliforme	Rahim and Tawfig (1984)
	Fusarium solani	Jamil et al. (1983)
	Fusarium roseum	Freeman et al. (1978)
	Myrothecium roridum	Freeman et al. (1978)

(Continued)

Table 3 (Continued)

Plant Species	Fungus	Reference
Eichhornia crassipes (Continued)	*Mycoleptodiscus terrestris*	Horst (1979)
	Nigrospora sp.	Charudattan (1973)
	Phoma sorphina	Rahim and Tawfig (1984)
	Pythium sp.	Charudattan (1973)
	Rhizoctonia sp.	Freeman (1977)
	Sigmoidea sp.	Lin and Charudattan (1975)
	Uredo eichhorniae	Freeman et al. (1981)
	Trichoderma sp.	Freeman et al. (1981)
Eleocharis acicularis	*Claviceps nigricans*	Conners (1967)
Eleocharis palustris	*Puccinia eleocharidis*	Conners (1967)
Eleocharis parvula	*Leptosphaeria culmorum*	Conners (1967)
Eleocharis pauciflora	*Septoria punctoidea*	Conners (1967)
Elodea canadensis	*Alternaria tenuissima*	Bernhardt (1983)
	Phythium afertile	Berhnardt (1983)
Hydrilla verticillata	*Aspergillus awomori*	Pennington (1985)
	Aspergillus sp.	Freeman (1977)
	Cephalosporium	Charudattan (1973)
	Chaetophoma sp.	Charudattan (1973)
	Curvularia sp.	Varghese and Singh (1973)
	Fusarium roseum	Charudattan et al. (1984)
	Fusarium solani	Charudattan et al. (1978)
	Gliocephalis	Charudattan et al. (1978)
	Humicola sp. w.	Pennington (1985)
	Trichoderma sp.	Pennington (1985)
	Oidiodendron sp.	Charudattan (1973)
	Penicillium sp.	Freeman (1977)
	Periconia sp.	Charudattan (1973)
	Phoma sp.	Charudattan (1973)
	Phytopthora parasitica	Freeman (1977)
	Phythium sp.	Varghese and Singh (1973)
	Rhizoctonia solani	Joyner and Freeman (1973)
	Sclerotium rolfsi	Freeman (1977)
	Stigmina sp.	Charudattan (1973)

(Continued)

Table 3 (Continued)

Plant Species	Fungus	Reference
Hydrilla verticillata (Continued)	*Trichoderma* sp.	Freeman (1977)
	Verticillium sp.	Varghese and Singh (1973)
Myriophyllum spicatum	*Acremonium curvulum*	Andrews et al. (1982)
	Alternaria tenuissima	Bernhardt (1983)
	Cephalosporium sp.	Bernhardt (1983)
	Chaetomium funicolum	Bernhardt (1983)
	Cylindrocarpon sp.	Bernhardt (1983)
	Dactylella microaquatica	Hayslip and Zettler (1973)
	Epicoccum nigrum	Bernhardt (1983)
	Flagellospora curvula	Bernhardt (1983)
	Flagellospora stricta	Hayslip and Zettler (1973)
	Fusarium moniliforme	Hayslip and Zettler (1973)
	Fusarium nivale	Bernhardt (1983)
	Fusarium oxysporium	Hayslip and Zettler (1973)
	Fusarium roseum	Hayslip and Zettler (1973)
	Fusarium solani	Hayslip and Zettler (1973)
	Fusarium sporotrichoides	Andrews and Hecht (1981)
	Fusarium tricinctum	Bernhardt (1983)
	Gliocladium roseum	Bernhardt (1983)
	Jycoleptodiscus terrestris	Gunner (1983)
	Phoma sp.	Bernhardt (1983)
	Physoderma sp.	Sparrow (1974)
	Pythium afertile	Bernhardt (1983)
	Pythium carolinianum	Bernhardt (1983)
	Rhizoctonia solani	Freeman et al. (1981)
	Sclerotium hydrophyllum	Hayslip and Zettler (1973)
	Trichoderma sp.	Bernhardt (1983)
	Trichothecium sp.	Andrews (1980)
Najas flexilis	*Rhizoctonia solani*	Bourn and Jenkins (1928)

(Continued)

Table 3 (Continued)

Plant Species	Fungus	Reference
Nuphar advena	*Entyloma nymphaeae*	Index of Plant Diseases
	Mycosphaerella pontederiae	Index of Plant Diseases
	Phyllosticta fatiscens	Index of Plant Diseases
	P. nymphaeacea	Index of Plant Diseases
	Sporobolomyces roseus	Conners (1967)
Nuphar luteum	*Cercospora numphaeacea*	Charudattan et al. (1978)
	Dichotomophothoropsis numphaerum	Johnson and King (1976)
	Pythium sp.	Van der Velde (1978)
	Sclerotium sp.	Johnson et al. (1976)
Nymphaea odorata	*Alternaria* sp.	Horst (1979)
	Cercospora exotica	Horst (1979)
	Cercospora nymphaeacea	Index of Plant Diseases
	Dichotomophothoropsis numphaearum	Johnson and King (1976)
	Entyloma numphaeae	Index of Plant Diseases
	Mycosphaerella pontederiae	↓
	Ovularia nymphaerum	↓
	Phyllosticta fatisscens	↓
	Pythium sp.	↓
	Sclerotium sp.	Johnson et al. (1976)
Nymphaea tuberosa	*Dichotomophothoropsis numphaerum*	Johnson and King (1976)
	Entyloma numphaeae	Index of Plant Diseases
	Gleosporium numphaearum	Conners (1967)
	Pythium sp.	Index of Plant Diseases
Nymphoides peltata	*Puccinia scirpi*	Munda and Garrasi (1978)
	Septoria villarsiae	Munda and Gerrasi (1978)
Nymphoides cordata	*Burrillia decipiens*	Conners (1967)
	Burrillia limnanthemi	Conners (1967)
Oenanthe sarmentosa	*Nyssopsora echinata*	Conners (1967)
	Septoria oenanthis	Conners (1967)
Phragmites communis	*Claviceps purpurea*	Index of Plant Diseases
	Graphyllium graminis	↓
	Hendersonia arundinacea	↓
	Mycosphaerella sp.	↓

(Continued)

Table 3 (Continued)

Plant Species	Fungus	Reference
Phragmites communis (Continued)	*Napicladium arundinaceum*	Index of Plant Diseases
	Neovossia iowensis	
	Papularia arundinis	
	Puccinia mognusiana	
	Puccinia phragmitis	
	Pythium debaryanum	
	Pythium ultimum	
	Scolecotrichum graminis	
	Selenophoma graminis	
	Stagonospora spp.	
Pistia stratiotes	*Rhizoctonia solani*	Joyner and Freeman (1973)
Pontederia lanceolata	*Rhizoctonia solani*	Joyner and Freeman (1973)
	Uromyces pontederiae	Charudattan (1981)
Pontederia cordata	*Cercospora pontederiae*	Conners (1967)
Potamogeton crispus	*Coniothyrium* sp.	Bernhardt (1983)
	Dactylella aquatica	Bernhardt (1983)
	Geotrychium sp.	Bernhardt (1983)
	Papulaspora aspera	Bernhardt and Duniway (1985)
	Pythium afertile	Bernhardt (1983)
	Trichoderma sp.	Bernhardt (1983)
Potamogeton natans	*Doassansia hydrophila*	Lowe (1969)
Potamogeton nodosus	*Curvularia* sp.	Bernhardt (1983)
	Doassansia martanoffiana	Conners (1967)
	Papulaspora aspera	Bernhardt and Duniway (1985)
	Pythium sp.	Bernhardt (1983)
Potamogeton pectinatus	*Anquilospora crassa*	Bernhardt (1983)
	Cephalosporium sp.	Bernhardt (1983)
	Curvularia sp.	Lumsden et al. (1963)
	Diplosporium sp.	Bernhardt (1983)
	Flagellospora curvula	Bernhardt (1983)
	Fusarium moniliforme	Bernhardt (1983)

(Continued)

Table 3 (Continued)

Plant Species	Fungus	Reference
Potamogeton pectinatus	*Hyaloflorae* sp.	Lumsden et al. (1963)
	Nigrospora oryzae	Bernhardt (1983)
	Phoma sp.	Lumsden et al. (1963)
	Pullaria pullulans	Lumsden et al. (1963)
	Pythium afertile	Bernhardt (1983)
	Pythium carolinianum	Bernhardt (1983)
	Pythium sp.	Lumsden et al. (1963)
	Rhizoctonia solani	Bourn and Jenkins (1928)
Potamogeton perfoliatus	*Cephalosporium* sp.	Motta (1978)
	Papulaspora sp.	Motta (1978)
	Pythium sp.	Motta (1978)
	Rhizoctonia solani	Bourn and Jenkins (1928)
	Trichoderma viride	Motta (1978)
Potamogeton sp.	*Doassansia martianoffiana*	Index of Plant Diseases
	D. occulta	
	Lagenidium muenschari	
	Ramularia aquatilis	
	Rhizoctonia solani	
Ruppia cirrhosa	*Tetramyxa parasitica*	Verhoeven (1975)
Ruppia maritima	*Cephalosporium* sp.	Motta (1978)
	Papulospora sp.	Motta (1978)
	Pythium sp.	Motta (1978)
	Rhizoctonia solani	Bourn and Jenkins (1928)
	Trichoderma viride	Motta (1978)
Salvinia auriculata	*Alternaria* sp.	Loveless (1969)
	Spicariopsis sp.	Loveless (1969)
Salvinia rotundifolia	*Rhizoctonia solani*	Joyner and Freeman (1973)
Sagittaria sp.	*Cercospora alismatis*	Horst (1979)
	Cercospora sagittariae	Conners (1967)
	Didymaria alismatis	
	Gleosporium confluens	
	Marssonina sp.	
	Burrillia pustulate	
	Doassansia deformans	
	Doassansia furva	
	Doassansia intermedia	

(Continued)

Table 3 (Concluded)

Plant Species	Fungus	Reference
Sagittaria sp. (Continued)	*Doassansia obscura*	Conners (1967)
	Doassansia opaca	
	Doassansia sagittariae	
	Fusarium acuminatum	
	Rhynchosporium alismatis	
Scirpus articulatus	*Physoderma thilumalacharii*	Pavgi and Singh (1980)
Scirpus sp.	*Heterosporium*	Lowe (1969)
Spartina alterniflora	*Buergenerula spartinae*	Torzilli and Andrykovitch (1980)
	Sphaerulina pedicellata	Gessner et al. (1972)
	Uromyces acuminatus	Conners (1967)
Spirodela polyrhiza	*Tracya lemnae*	Conners (1967)
Typha latifolia	*Cladosporium* spp.	Index of Plant Diseases
	Cryptomela typhae	Index of Plant Diseases
	Hendersonia typhae	Index of Plant Diseases
	Heterosporium maculatum	
	Hymenopsis hydrophila	
	Leptosphaeria eustoma	Lowe (1969)
	Leptosphaeria typharum	Index of Plant Diseases
	Lophodermium typhinum	
	Mycosphaerella typhae	
	Ophiobolus sp.	Horst (1979)
	Phyllosticta typhina	Index of Plant Diseases
	Pleospora typhae	
	Pythiogeton autossytum	
	Pythium helicoides	
	Scolecotrichium typhae	
	Stagnospora typhiodearum	
Vallisneria spiralis	*Rhizoctonia solani*	Bourn and Jenkins (1928)
Zostera marina	*Acremonium* sp.	Newel (1981)
	Cladosporium sp.	Newel (1981)
	Labyrinthula sp.	Renn (1936)
	Lulworthia sp.	Newel (1981)
	Ophiobolus halimus	Tutin (1938)

Table 4

List of Selected Plant-Parasitic Nematodes

Associated with Aquatic Plants

Plant Species	Nematode	Reference
Alisma plantago aquatica	*Heterodera aquatica*	Gerber et al. (1986b)
Alternanthera phyloxeroides	*Cacopaurus*	Esser et al. (1985)
	Criconemoides	
	Dolichodorus	
	Helicotylenchus crenacauda	
	Helicotylenchus erythrinae	
	Heterodera marioni	Plakidas (1936)
	Meloidogyne sp.	Index of Plant Diseases
	Pratylenchus	Esser et al. (1985)
	Trichodorus proximus	Esser et al. (1985)
	Tylenchus	Esser et al. (1985)
	Xiphinema	Esser et al. (1985)
Ceratophyllum demersum	*Aphelenchoides fragariae*	Smart and Esser (1968)
	Aphelenchoides sp.	Gerber et al. (1986a)
	Criconemoides sp.	
	Hirschmanniella caudacrena	
	Hirschmanniella sp.	
	Hopolaimus tylenchiformis	
	Pratylenchus sp.	
	Trichodorus sp.	
	Tylenchus sp.	
Eichhornia crassipes	*Xiphidorus amazonensis*	Gerber et al. (1986b)
Eleocharis acicularis	*Helicotylenchus* sp.	
	Heterodera canadensis	
	Meloidogyne sewelli	
Eleocharis palustris	*Meloidogyne* sp.	
Eleocharis sp.	*Doplichodorus similis*	
Elodea canadensis	*Anguillula* sp.	
	Aphelenchus sp.	
	Hirschmanniella oryzae	
Hydrilla verticillata	*Aphelenchoides fragariae*	Gerber et al. (1986a)
	Aphelenchoides sp.	
	Criconemoides sp.	

(Continued)

Table 4 (Continued)

Plant Species	Nematode	Reference
Hydrilla verticillata (Continued)	*Dolichodorus* sp.	Gerber et al. (1986a)
	Helicotylenchus sp.	
	Hirschmanniella caudacrena	
	Hirschmanniella gracilis	
	Hirschmanniella oryzae	
	Hirschmanniella sp.	
	Trichodorus sp.	
	Thylenchorhynchus irregularis	
	Tylenchus sp.	
	Xiphinema americanum	
Lemna sp.	*Aphelenchoides fragariae*	Smart and Esser (1968)
Limnobium spongia	*Aphelenchoides fragariae*	Esser et al. (1985)
Lythrum salicaria	*Meloidogyne* sp.	Gerber et al. (1986b)
Myriophyllum aquaticum	*Aphelenchoides* sp.	Esser et al. (1985)
	Hirschmanniella sp.	Esser et al. (1985)
Myriophyllum spicatum	*Aphelenchoides fragariae*	Gerber et al. (1986b)
	Hirschmanniella gracilis	Gerber et al. (1986b)
Myriophyllum verticillatum	*Ditylenchus dipsaci*	Gaevskaya (1969)
Najas flexilis	*Aphelenchoides fragariae*	Gerber et al. (1986b)
Najas spp.	*Aphelenchoides fragariae*	Smart and Esser (1968)
	Hirschmanniella caudacrena	Esser et al. (1985)
Nuphar luteum	*Chronogaster*	Prejs (1977)
	Chrysonemoides	
	Dorylaimoides	
	Plectus	
	Tobrilus	
	Tripyla	
Nymphaea sp.	*Criconemoides*	Esser et al. (1985)
	Dolichodorus heterocephallus	
	Helicotylenchus	
	Meloidogyne	
	Pratylenchus	
	Rotylenchus	
	Trichodorus	

(Continued)

Table 4 (Continued)

Plant Species	Nematode	Reference
Oenanthe sp.	*Meloidogyne marioni*	Gaevskaya (1969)
Phragmites communis	*Anguina graminis*	Gaevskaya (1969)
	Ditylenchus radicicola	Gerber et al. (1986b)
	Dolichodorus sp.	Gerber et al. (1986b)
	Helicotylenchus erythrinae	Gerber et al. (1986b)
	Hirschmanniella gracilis	Gerber et al. (1986b)
Pistia stratiotes	*Hirschmanniella caudacrena*	Esser et al. (1985)
Pontederia lanceolata	*Dolichodorus*	Esser et al. (1985)
	Tylenchorhynchus	Esser et al. (1985)
Potamogeton friesii	*Ditylenchus dipsaci*	Gaevskaya (1969)
Potamogeton lucens	*Calolaimus*	Prejs (1986)
	Chromadorita	Prejs (1977)
	Chronogaster	Prejs (1977)
	Chrysonemoides	Prejs (1977)
	Cryptonchus	Prejs (1986)
	Dorylaimoides	Prejs (1977)
	Dorylaimus	
	Hirschmanniella	
	Panagrolaimus	
	Plectus	
	Tobrilus	
	Tripyla	
Potamogeton pectinatus	*Hirshmanniella*	Prejs (1986)
	Panagrolaimus	
	Plectus	
Potamogeton perfoliatus	*Calolaimus*	
	Chronogaster	
	Chrysonemoides	
	Hirschmanniella	
	Cryptonchus	
	Panagrolaimus	
	Plectus	
Potamogeton sp.	*Aphelenchoides fragariae*	Smart and Esser (1968)
Ruppia maritima	*Aphelenchoides*	Esser et al. (1985)
	Helicotylenchus	
	Hirschmanniella gracilis	

(Continued)

Table 4 (Concluded)

Plant Species	Nematode	Reference
Ruppia maritima (Continued)	*Hirschmanniella oryzae*	Esser et al. (1985)
	Tylenchus	Esser et al. (1985)
Sagittaria sagittifolia	*Chrysonemoides*	Prejs (1977)
	Dorylaimus	Prejs (1977)
	Plectus	Prejs (1977)
Sagittaria sp.	*Aphelenchoides*	Esser et al. (1985)
	Dolichodorus	
	Helicotylenchus	
	Hirschmanniella caudacrena	
	Scutellonema	
	Tylenchus	
	Xiphinema	
Sirpus americanus	*Hirschmanniella anchoryzae*	Gerber et al. (1986b)
	Hirschmanniella gracilis	Gerber et al. (1986b)
Spartina alterniflora	*Oncholaimus*	Gessner et al. (1972)
	Meloidogyne spartinae	Gerber et al. (1986b)
Typha sp.	*Criconemoides mutabile*	Siddiqui et al. (1973)
	Dolichodorus spp.	
	Helicotylenchus pseudorobustus	
	Hemicriconemoides sp.	
	Hemicycliophora sp.	
	Heterodera sp.	
	Hirschmanniella belli	
	Hirschmanniella spinicaudata	
	Hirschmanniella sp.	
	Medloidogyne marioni	Gaevskaya (1969)
	Pratylenchus neglectus	Siddiqui et al. (1973)
	Pratylenchus thornei	
	Trichodorus sp.	
	Thylenchorhynchus clarus	
	Tylenchulus semipenetrans	
Vallisneria americana	*Hirschmanniella caudacrena*	Esser et al. (1985)
	Tylenchorhynchus irregularis	Gerber et al. (1986b)
	Tylenchus sp.	Gerber et al. (1986b)
	Xiphinema americanum	Gerber et al. (1986b)

Table 5

Senescence-Inducing Factors

Inducing Factor	Manipulation in the Field*	
	Feasible	Infeasible
Low light	++	
Nutrient availability		+
Photoperiod	++	
Temperature		+
Dense periphyton	+	
External growth regulators (ABA)	++	
Sublethal herbicide doses	+++	
Herbivores	++	

* + = low, ++ = high, +++ = higher feasibility.

APPENDIX A: GLOSSARY*

Commensalism--The living together of two or more organisms with benefit usually to one and without injury to either.

Decomposition--Degradation (often microbial) of dead and organic matter.

Disease--Injurious alteration of one or more ordered processes of energy utilization in a living system caused by the continued irritation of a primary causal factor or factors.

Epiphytic--Being attached to the surface of an organism (plant).

Epiphyton--The assemblage of (micro)organisms that grow attached to aquatic macrophytes.

Epiphytotic--Relating to a widespread and destructive disease of plants (epidemic).

Host (suscept)--The plant that is being acted on by a pathogen.

Host range of pathogen--The kinds of plants a specific pathogen can infect and cause disease or set up an infection process.

Infection--The process in which a parasite or biotic pathogen establishes contact with the host tissues.

Infectious diseases--Those caused by living organisms (e.g., fungi or bacteria) in contrast to noninfectious disease caused by nonliving pathogens (air pollutants).

Inoculum--The infective unit or propagule (e.g., the spore) that is carried to the host plant and initiates infection.

Parasite--An organism that obtains food from another living organism (host).

Pathogenesis--Process of disease development in the host.

Pathogenicity--The ability of a pathogen to produce disease in a given host.

Pathogens--Factors or agents that cause plant disease; may be living (biotic) or nonliving (abiotic).

Periphyton--Assemblage of organisms growing upon free surfaces of submerged objects in water (corresponds to the German term "Aufwuchs," which is often used in English terminology).

Saprophyte--An organism that can obtain nutrients from dead organic material.

Senescence--The final phase in development of an organism leading to cellular breakdown and death.

Symptoms--Outward manifestations of disease.

Vector--An agent (biotic or abiotic) able to transmit a pathogen.

Virulence--The degree of pathogenicity.

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* Based on definitions given by Hanson (1957), Holcomb (1982), Lucas et al. (1985), and Sladeckova (1962).